FRDA Report 093

Autecology, Biology, Competitive Status and Response to Treatment of Seven Southern Interior Weed Species

A Literature review updating portions of:
Autecological Characteristics of Selected Species that Compete with Conifers in British Columbia: A Literature Review
Land Management Report Number 33
by S. Haeussler and D. Coates, 1986

by
Philip G. Comeau[1], Susan B. Watts[2], Caroline L. Caza[2],
John Karakatsoulis[2], Sandra M. Thomson[2], and Ann B. McGee[2]

[1] B.C. Ministry of Forests,
Research Branch,
31 Bastion Square,
Victoria, B.C. V8W 3E7

[2] Faculty of Forestry,
University of British Columbia,
270-2357 Main Mall,
Vancouver, B.C. V6T 1W5

August 1989

ISSN 0835 0752

ECONOMIC & REGIONAL DEVELOPMENT AGREEMENT

Canada BC

90-01774/

Funding for this publication was provided by the Canada-British Columbia Forest Resource Development Agreement - a five year (1985-90) $300 million program cost-shared equally by the federal and provincial governments.

Canadian Cataloguing in Publication Data

Main entry under title:
Autecology, biology, competitive status and response to treatment of seven southern interior weed species

(FRDA report, ISSN 0835-0752 ; 093)

"A literature review updating portions of: Autecological characteristics of selected species that compete with conifers in British Columbia: a literature review; Land management report number 33, by S. Haeussler and D. coates, 1986."

Issued under Canada-BC Forest Resource Development Agreement.
Co-published by B.C. Ministry of Forests.
"Canada/BC Economic & Regional Development Agreement."
Includes bibliographical references.
ISBN 0-7726-1021-5

1. Forest ecology - British Columbia. 2. Conifers - Diseases and pests - British Columbia. 3. Plant competition - British Columbia. 4. Conifers - British Columbia - Seedlings. I. Comeau, P. G., 1954- II. Canada. Forestry Canada. III. Haeussler, S. (Sybille). Autecological characteristics of selected species that compete with conifers in British Columbia. IV. British Columbia. Ministry of Forests. V. Canada-British Columbia Forest Resource Development Agreement. VI. Canada/BC Economic & Regional Development Agreement. VII. Series.

QK938.F6A97 1989 581.5'264'09711 C89-092248-9

© 1989 Government of Canada,
Province of British Columbia

This is a joint publication of Forestry Canada and the British Columbia Ministry of Forests.

Produced and distributed by the Ministry of Forests, Research Branch.

For additional copies and/or further information about the Canada-British Columbia Forest Resource Development Agreement, contact:

Forestry Canada
Pacific Forestry Centre
506 West Burnside Road
Victoria, B.C. V8Z 1M5
(604) 388-0600

or

B.C. Ministry of Forests
Research Branch
31 Bastion Square
Victoria, B.C. V8W 3E7
(604) 387-6719

TABLE OF CONTENTS

INTRODUCTION 1
Biogeoclimatic zone abbreviations 1

LITERATURE REVIEW 2
Alnus viridis ssp. *sinuata* (Sitka alder) 2
Betula papyrifera (paper birch) 5
Calamagrostis rubescens (pinegrass) 12
Epilobium angustifolium (fireweed) 16
Menziesia ferruginea (false azalea) 21
Rhododendron albiflorum (white-flowered rhododendron) 25
Rubus parviflorus (thimbleberry) 30

LITERATURE CITED 34

INTRODUCTION

This report contains a literature review of the autecology and competitive status of seven species that compete with conifer seedlings in the Southern Interior of British Columbia.

The seven species are:

Alnus viridis ssp. *sinuata*	Sitka alder
Betula papyrifera	paper birch
Calamagrostis rubescens	pinegrass
Epilobium angustifolium	fireweed
Menziesia ferruginea	false azalea
Rhododendron albiflorum	white-flowered rhododendron
Rubus parviflorus	thimbleberry

This literature review updates Haeussler and Coates (1986) and closely follows their format. In some instances, when no new information could be found, the Haeussler and Coates text was included without change. The review, along with information that has been published since 1987, will be incorporated into a new edition of Haeussler and Coates, to be released in early 1990.

This update is based on published references, located through computerized searches of CAB (Commonwealth Agricultural Bureau on-line database) and BIOSIS (Biological Abstracts on-line database), as well as in published bibliographies and other literature reviews. The authors of this review have tried to include all pertinent English language publications which were published up to, and including, 1987.

Readers who are aware of any relevant publications that have not been included here or readers who would like to obtain copies of any reference material included in the literature review, are asked to contact Dr. Susan Watts (University of British Columbia, Faculty of Forestry, 270-2357 Main Mall, Vancouver, BC V6T 1W5; phone: 604-228-6316).

Financial support for this project was provided by the cost-shared component of the Canada-British Columbia Forest Resource Development Agreement, Extension, Demonstration, Research and Development sub-program under project 3.41.

Biogeoclimatic zone abbreviations

Abbreviation	Biogeoclimatic zone
AT	Alpine Tundra
BG	Bunchgrass
BWBS	Boreal White and Black Spruce
CDF	Coastal Douglas-fir
CWH	Coastal Western Hemlock
ESSF	Engelmann Spruce - Subalpine fir
ICH	Interior Cedar - Hemlock
IDF	Interior Douglas-fir
MS	Montane Spruce
MH	Mountain Hemlock
PP	Ponderosa Pine
SWB	Spruce - Willow - Birch
SBPS	Sub-boreal Pine - Spruce
SBS	Sub-boreal Spruce

LITERATURE REVIEW

Alnus viridis ssp. *sinuata* (Regel) Love & Love — Sitka alder

DESCRIPTION

Sitka alder is a deciduous plant that grows as either a tall shrub or small tree. As a tree, it has a slender trunk with an open crown of short horizontal branches and a shallow root system. On favourable sites, Sitka alder can attain a height of 12 m and a stem diameter of 20 cm (Hosie 1979). Leaves are oval with toothed margins. Twigs are slender and reddish brown, and have buds without stalks. Both male and female catkins are borne on long stalks, and a small wing nutlet is produced (Brayshaw 1978; Hosie 1979).

DISTRIBUTION AND ABUNDANCE

Sitka alder is a transcontinental species, distributed primarily in the northern coniferous forests (Brayshaw 1978). In British Columbia, it is found as far north as the Yukon border and south to the American border. It is absent in the northeastern part of the province where it is replaced by green alder (*Alnus viridis*) (Krajina *et al.* 1982). Its distribution includes most of the biogeoclimatic zones of British Columbia: ESSF, SBS, IDF, ICH, MH, and higher elevations of the CDF and CWH (Krajina *et al.* 1982; Klinka and Scagel 1984).

Altitudinal Range: In British Columbia, Sitka alder is found from 100 m to timberline (Brayshaw 1978; Binkley 1982). In Alaska, Mitchell (1968) has reported finding shrub Sitka alder growing at up to 1025 m in elevation.

HABITAT

Climatic Relations: While Sitka alder is found under various climatic regimes in British Columbia, it grows best under cool and moist (Hosie 1979), well-drained conditions (Brayshaw 1978). It is primarily a subalpine-boreal species, but is also found in montane-boreal, cool temperate, warm temperate, and cool mesothermal climates (Klinka and Scagel 1984).

Site and Soil Conditions: Sitka alder is able to colonize disturbed sites such as clearcuts where the mineral soil has been exposed. It also occurs on subalpine avalanche tracks (Krajina *et al.* 1982) and on recently exposed mineral materials left by retreating glaciers, where it is one of the first species to reinvade the site. Its symbiotic relationship with nitrogen-fixing bacteria allows it to occupy many disturbed sites, such as coal mine spoils (Heilman and Ekuan 1982), which are low in nitrogen.

Nutrient Relations: All alder species grow in symbiosis with nitrogen-fixing bacteria of the genus *Frankia* (Benecke 1970; Dalton and Naylor 1975; Carpenter *et al.* 1979; Carpenter and Robertson 1984). This enables Sitka alder to invade relatively sterile soils. Nitrogen fixation rates range from 20 to 150 kg/ha per year (Binkley 1982; Heilman and Ekuan 1982). Binkley (1984) was able to demonstrate an increase in total N and available N, extractable P, Ca, and Mg in the top 10 cm of mineral soil of a Sitka alder stand as compared to a non-alder stand in the same area. An increase in soil C under Sitka alder stands was also reported by Bollen *et al.* (1969) and Tarrant (1983). Krajina *et al.* (1982) describe Sitka alder as a calciphytic plant with high requirements for Mg, P, K, and Ca. Soil pH under Sitka alder stands tends to vary according to soil fertility (Binkley 1984), but in general soils tend to be acidic (Mitchell 1968).

Water Relations: Sitka alder grows best under fresh to wet conditions (Klinka and Scagel 1984), and is rarely found on very dry sites. Cline and Campbell (1976) found that it was not able to maintain osmotic potentials below -16 bars, which restricted it to wetter sites. As well, Shipton and Burggraaf (1982) reported a decline in the growth of *Frankia* isolates at water potentials below -2 to -5 bars.

Its high flood tolerance (Krajina *et al.* 1982) allows Sitka alder to grow along stream edges and on alluvial floodplains.

Light Relations: The light requirements of Sitka alder vary by site. Where moisture is not limiting, this species can grow under full sunlight to moderately shaded conditions (Krajina *et al.* 1982; Klinka and Scagel 1984), making it a suitable understory N-fixing species in open-grown coniferous plantations (Gordon and Dawson 1979; Harrington and Deal 1982; Binkley *et al.* 1984). The relationship between light levels and N-fixation rates is not known for Sitka alder, but Dawson and Gordon (1979) reported a positive, linear relationship between photosynthetic rate and total plant nitrogen for *A. glutinosa*. This suggests that at low light levels, such as that found under a dense forest canopy, the rate of N-fixation by *A. glutinosa* would be greatly reduced. Light reaching the understory depends on the structure of the canopy, in particular the overstory leaf area. Thus, any factor(s) that affect the overstory leaf area, such as moisture and nutrient availability, will affect the nitrogen fixation rates of understory species such as Sitka alder.

Temperature Relations: Sitka alder is a frost-resistant species (Krajina *et al.* 1982), able to grow in most parts of British Columbia. Its ability to fix nitrogen is more temperature-limited. Benecke (1970) found maximum N-fixation rates of *A. viridis* to occur at soil temperatures of 25°C, and no N-fixation at temperatures below 5°C.

GROWTH AND DEVELOPMENT

Compared to red alder (*A. rubra*), Sitka alder is not considered a fast-growing species. It can grow 1 m in 10 years on a high-elevation (1160 m) site , to 4.5 m in 10 years on a low-elevation (625 m) site (Harrington and Deal 1982). At higher elevations, height growth is restricted by snowpress (Lyons 1952).

Phenology: Sitka alder produces male and female flowers in narrow catkins about 10 cm long. Flowering occurs between May and June. Cones are usually ripe by mid-September, with seed dispersal following shortly thereafter (Viereck and Little 1972).

REPRODUCTION

Seed Production and Dispersal: Sitka alder begins to produce seed at about 6-8 years of age with optimum production occurring at about age 25. It produces ample seed every year with bumper crops every 3-5 years. Dissemination of seeds is primarily by wind. The narrowly winged nutlets can be carried great distances (Fowells 1965; USDA 1974; Kenady 1978; Burns 1983).

Seed Viability and Germination: There is little information on Sitka alder seed viability, but Zasada *et al.* (1983) reported 40% seed viability for *A. crispa*. Germination, depending on microsite, occurs throughout the summer. Germination of *A. crispa* seeds has been found to be greatest on sites that have been heavily burned (Zasada *et al.* 1983).

Vegetative Reproduction: Sitka alder will sprout from cut stems, but the predominant method for reproduction is through seed production.

RANGE AND FORAGE VALUES

Sitka alder is of limited value as browse for wildlife (Elias 1980). Whitetail deer will feed on the leaves and twigs, and some birds will feed on the seeds. In southern Alaska, Sitka alder provides cover for moose and bear (Mitchell 1968).

EFFECTS ON CROP TREES

Competition: The low bushy habit and slow growth rate of Sitka alder make it a less serious brush problem than red alder (Binkley 1982; Harrington and Deal 1982). On moist sites, a dense Sitka alder canopy may shade out commercial conifer seedlings such as Douglas-fir (Harrington and Deal 1982). Under these conditions, planting large conifer stock may aid in plantation establishment. In

areas with moderate to high snowfall, Sitka alder may physically damage overtopped conifers as a result of snowpress.

Beneficial Effects: On dry, south-facing slopes, Sitka alder may reduce heat stress experienced by conifer seedlings by providing them with shade, although there may be an increase in moisture competition. The ability of Sitka alder to increase soil nitrogen content is the major benefit of this species to forest plantations and forest productivity. Recent studies have shown that Sitka alder can fix between 20 and 150 kg ha^{-1} $year^{-1}$ of nitrogen (Binkley 1982; Heilman and Ekuan 1982; Binkley *et al.* 1984). Sitka alder's shrubby growth form and its ability to grow in the understory of conifer plantations make it a desirable nurse species if it is not too dense (Harrington and Deal 1982; Binkley *et al.* 1984).

Comparing two stands of 23-year-old Douglas-fir, one growing with Sitka alder in the understory and one growing without, Binkley *et al.* (1984) reported greater Douglas-fir stem biomass increment and current 5-year average basal area growth on the Sitka alder site. Heilman (1983) reported an increase in the first 5 years of Douglas-fir seedling growth on coal mine spoils when planted with Sitka alder, although growth differences were not evident after 5 years. Harrington and Deal (1982) suggested that conifers such as Douglas-fir could benefit most from Sitka alder interplanting on sites that are initially low in total nitrogen and organic matter content.

On avalanche tracks, Sitka alder is an early colonizer. It aids in stabilizing steep slopes and preventing erosion (Hosie 1979; Marchant and Sherlock 1984).

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: In north-central British Columbia, invasion of Sitka alder after clearcutting can be slow. Eis (1981) reported that alder cover increased slightly over the first 6 years after harvesting, with the greatest cover levels (10%) occurring on alluvial sites. In mature lodgepole pine forests of central Alberta, green alder (*A. crispa*) can form a dense understory (2-3 m tall), especially on moist sites (Corns and La Roi 1976), but usually accounts for less than 4% of the understory community. On these sites, green alder showed a significant decrease in percent cover after clearcutting. This may be due in part to the increase in competition from herbaceous plants (44% cover) (Corns and La Roi 1976).

Fire: Broadcast burning in the Cedar-Hemlock Zone of northern Idaho favoured Sitka alder establishment (Mueggler 1965). Increased percent cover of Sitka alder was evident on sites that had a history of repeated burns. Pojar *et al.* (1982) suggest that Sitka alder's ability to fix nitrogen make it a favourable species on sites that have had much of the organic matter removed as a result of intense fires.

Herbicides: Spraying with glyphosate at 3 kg a.i./ha followed by burning gave very effective control of Sitka alder (Expert Committee on Weeds 1985). Treatment of Sitka alder with hexazinone has yielded variable responses (Expert Committee on Weeds 1985).

Soil Disturbance: Sitka alder is usually associated with soil disturbances. In Alaska, Sitka alder is one of the first species to invade recently exposed glacial deposits (Crocker and Major 1955; Crocker and Dickson 1957; Ugolini 1968). Avalanche tracks in mountainous terrain are also quickly occupied by Sitka alder (Bollen *et al.* 1969).

Betula papyrifera Marsh. — Paper birch

(white birch, canoe birch)

DESCRIPTION

Paper birch is a small to medium-sized deciduous tree up to 30 m tall and 10-30 cm in diameter (Watson *et al.* 1980). It is considered one of the most variable tree species in Canada (Brayshaw 1978). The bark is variously coloured: most commonly it is white or cream with conspicuous brown, horizontally elongated lenticels, and it peels readily in sheets (Brayshaw 1978; Watson *et al.* 1980; Angove and Bancroft 1983). The bark may be copper-brown in colour (Angove and Bancroft 1983). The crown is oval and columnar, with ascending branches and dark brown branchlets (Brayshaw 1978), and is often multi-stemmed. The twigs are fairly slender, pubescent (often becoming smooth later on) or occasionally glandular, with whitish lenticels (Hosie 1966; Brayshaw 1978). The leaves are narrowly egg-shaped to nearly round (5-9 cm long) (Brayshaw 1978; Angove and Bancroft 1983) with simply or doubly serrated edges. The upper surface is dull green, and the undersides are paler and pubescent (Hosie 1966; Brayshaw 1978; Angove 1981). Both male and female catkins are pendulous when mature. The fruit is a tiny two-winged nut, with the wings broader than the body (Hosie 1966; Angove 1981).

Varieties: Several geographic varieties are described, and are difficult to recognize. The most common variety in British Columbia is var. *papyrifera* which occurs in the Interior (Brayshaw 1978). Other varieties found in the province are var. *commutata* which occurs commonly in the Lower Fraser Valley and on the coast, and var. *subcordata* which is the result of crossing between var. *papyrifera* and waterbirch (*Betula occidentalis*) (Brayshaw 1978). Paper birch also frequently crosses with *B. neoalaskana* and *B. pumila* (Brayshaw 1978). Brittain and Grant (1966, 1968) and Grant and Thompson (1975) provide detailed observations on paper birch varieties in British Columbia and the Rocky Mountains.

DISTRIBUTION AND ABUNDANCE

Paper birch has a transcontinental range in North America (Post *et al.* 1969; Viereck and Little 1972; Tang and Kozlowski 1982). It is widely distributed from northwestern Alaska, east across Canada to Labrador and Newfoundland, south in the northeastern states to Pennsylvania and Iowa, and in the western states to Montana and northeastern Oregon (Viereck and Little 1972). It is found throughout British Columbia, but is sporadic on the outer coast, absent in the Queen Charlotte Islands, and only found on the southeastern portion of Vancouver Island (Brayshaw 1978). Paper birch is common in most low- to medium-elevation biogeoclimatic zones in the Interior. It is commonly found in the BWBS, SBS, SBPS, and the ICH, and less commonly in the wetter CWH, PP, BG, IDF, and CDF zones (Krajina *et al.* 1982). It is absent from the ESSF, MH, SWB, and AT zones.

Altitudinal Range: Paper birch is found over a range of elevations (Post *et al.* 1969), but primarily occurs at low to moderate elevations. It does not occur in subalpine forests.

HABITAT

Climatic Range: Paper birch is adapted to a wide range of climates, occurring most frequently in montane-boreal and cool temperate climates, and less frequently in warm temperate and cool mesothermal climates (Klinka and Scagel 1984). It tolerates wide variations in the patterns and amounts of precipitation. It is extremely tolerant of cold, extending north almost to the limit of tree growth (Fowells 1965; Tang and Kozlowski 1982). Across its entire range, the climate is generally characterized by short cool summers and long cold winters with long periods of snow (Fowells 1965). In British Columbia, paper birch is especially abundant in areas of transitional climate, in the Coast/Interior ecotone, and between the dry and wet belts of the Interior. It apparently cannot compete well in the perhumid climate of the outer British Columbia coast, and is absent from most areas receiving extremely heavy snowloads.

Site and Soil Conditions: Paper birch is found on a wide range of soils, but appears to grow best on well-drained sandy or silty loams (Fowells 1965; Watson *et al.* 1980; Angove and Bancroft 1983). It is also common on shallow stony soils as well as organic soils. These soils are derived from a wide variety of parent materials, mainly glacial tills and outwash, ranging from acidic to highly calcareous (Fowells 1965). It is most abundant on rolling upland terrain or on alluvial sites, but is also found on open slopes, rock slides, bog and swamp margins, and along streams and river banks (Watson *et al.* 1980). It is common on burned or cut-over areas where it may form pure stands (Watson *et al.* 1980). Studies looking at the phytosociology of birch communities in southeast Labrador showed that these communities have very site-specific requirements, and are located in only the most favourable habitats, which are protected, very moist but well-drained slopes and seepages with shallow soils. Birch communities are absent from level, dry, or waterlogged sites (Foster 1984; Foster and King 1986).

Nutrient Relations: Paper birch is adapted to a wide variety of nutrient conditions (Post *et al.* 1969). The nutrient requirements are moderate to fairly high, especially for calcium and magnesium (Krajina *et al.* 1982), although other sources report low requirements for calcium and phosphorus and moderate requirements for sulphur and nitrogen (Watson *et al.* 1980). It appears to prefer nitrates as a nitrogen source, as it grows much better where nitrates are readily available (Krajina *et al.* 1982). Paper birch has a moderate tolerance for acidic conditions and will grow on highly calcareous soils (Fowells 1965), but it has been observed growing on soils of pH 3.2-4.4 (Watson *et al.* 1980). The trophotope (soil nutrient regime) that is most suitable for paper birch is nutrient-medium to nutrient-rich, and less frequently nutrient-poor or nutrient-very rich (Klinka and Scagel 1984).

Water Relations: Paper birch is described by some to be intolerant to flooding (Tang and Kozlowski 1982; Norby and Kozlowski 1983), whereas others describe it as highly tolerant to flooding and poorly drained soils (Krajina *et al.* 1982; Klinka and Scagel 1984). Flooding has been found to have severe effects on seedling growth and physiology (Tang and Kozlowski 1982; Norby and Kozlowski 1983). Ericsson and Schimpf (1986) showed an increase in the density of paper birch moving away from stream edges and on the steeper reaches of streams, and suggested that it is not tolerant of oxygen depletion in the rooting zone or of the soil modification resulting from flooding.

Paper birch is seldom found on very wet and poorly drained soils (Fowells 1965). Moist, well-drained soils are necessary for its establishment in southeast Labrador (Tang and Kozlowski 1982; Foster and King 1986). In British Columbia, paper birch is found on subxeric or submesic to subhygric sites (Angove and Bancroft 1983), or, according to Klinka and Scagel (1984), on fresh hygrotopes.

Light Relations: The shade tolerance of paper birch is relatively low (Fowells 1965; Hyvarinen 1968; Ohmann *et al.* 1978; Watson *et al.* 1980; Krajina *et al.* 1982; Klinka and Scagel 1984). Paper birch is common as an overstory tree in seral plant communities, but only survives one generation because of its shade intolerance (Hyvarinen 1968; Hosie 1973; Tang and Kozlowski 1982). It will occupy space in climax forests where gaps have been created by blowdown or other disturbances (Hyvarinen 1968). Seed germination has been found to be best under shaded (compared with full sunlight) conditions (Marquis *et al.* 1964; Horsley and Abbott 1970). Horsley and Abbott (1970) found that greater seedling mortality occurred in full sunlight compared with shaded conditions. It was also reported that greater early seedling growth occurred in 45% of full sunlight, while the lowest growth occurred in 13 and 100% of full sunlight. Subsequent seedling growth is favoured by full sunlight. Paper birch seedlings grown in full sunlight had larger roots, higher leaf weight, and a higher root-shoot ratio than those grown in partial shade (Marquis 1966). Germination rates under varying light conditions have been found to depend on seed sources, those from northern areas germinating more rapidly and achieving higher total germination than those from southern areas (Bevington 1986).

Temperature Relations: Paper birch is considered to be very frost tolerant, and it can easily endure solidly frozen ground (Watson *et al.* 1980; Krajina *et al.* 1982; Klinka and Scagel 1984). In Alaska, it grows on soils where the frost layer remains in the rooting zone through to early August (Foote 1983). Seasonal height growth will often begin while minimum temperatures are below freezing (Fowells 1965). Paper birch often colonizes coal spoil piles which are subject to high temperatures

(Watson *et al.* 1980), and in British Columbia appears able to tolerate very high summer temperatures as long as sufficient moisture is available. Bevington (1986) has found that seed source influences the range of temperatures over which germination occurs, with those from northern sources generally germinating over a wider range of temperatures and more rapidly at lower temperatures. The author pointed out that this germination response may be less related to latitude per se than to local climate and site-specific factors. Heninger and White (1974) found that paper birch seedlings grew well over a wide range of soil temperatures, but that total seedling biomass was highest between 19 and 30°C.

GROWTH AND DEVELOPMENT

Paper birch does not exhibit the rapid early growth characteristic of other hardwood species such as black cottonwood and alder. It is the initial growth period that is critical for paper birch regeneration (James and Courtin 1985). A number of factors influence initial seedling growth, and conditions that tend to favour germination often do not result in the best seedling growth (Marquis *et al.* 1964). The average height of paper birch seedlings in the first growing season is approximately 10 cm (Fowells 1965). A maximum height of 40 cm was achieved in the first growing season on favourable sites in full sunlight, but soil moisture interacted with the amount of available light (Marquis 1966). In British Columbia, average 3-year-old seedling height was reported to be 32 cm; in Alaska, the average height of 3-year-old seedlings was only 25 cm (Zasada *et al.* 1983).

Initial nutrient availability appears to be important in paper birch seedling growth. Four-year-old growth was very responsive to site condition, with a 220% range in above-ground production occurring over a range of sites (Chapin *et al.* 1983). Production was stimulated on sites with increased nutrient availability. Fowells (1965) reported 4-year-old seedlings with an average height of 1 m. Sprouts have more rapid growth compared with seedlings, growing up to 60 cm in the first growing season and twice as tall as seedlings after 4 years. The maximum height growth of paper birch is 30-40 m at maturity and 50-100 cm diameter at the base (Ohmann *et al.* 1978). Solomon and Leak (1969) have provided site index curves for New Hampshire paper birch stands.

Paper birch is a relatively short-lived tree species, usually reaching maximum production before 80 years of age (Post *et al.* 1969; Chapin *et al.* 1983). The maximum age of paper birch is approximately 115 years old, although ages of up to 200 years have been reported (Fowells 1965). Marks (1975) has studied the relationship between extension growth and the successional status of various deciduous trees of the northeastern U.S. He found that paper birch was intermediate in terms of successional status and extension growth characteristics. Extension growth of paper birch is indeterminate, occurring over half of the growing season.

Paper birch stands are distinguished by a lush, diverse understory, with no paper birch in smaller size classes present (Foster 1984). Where the seed source is abundant on nearby sites, stands may be dense on adjacent disturbed sites (Foster and King 1986). Paper birch does not reproduce well in established forests, and therefore only penetrates late stages of forest succession where gaps are created in the canopy following a disturbance such as blowdown (Hibbs 1982; Tang and Kozlowski 1982).

Radial growth of paper birch is responsive to changes in precipitation, temperature, and other factors that influence the amount of water stress experienced by trees (Braekke and Kozlowski 1975).

Stand deterioration occurs between 75 and 100 years of age, at which time the tops start to die, leaving a broken upper canopy (Foster and King 1986).

Phenology: Paper birch begins flowering in mid-April in southern areas and flowers during May and June in Alaska. Flowering takes place before the leaves expand. Height growth begins early in the growing season while temperatures are still quite cool; diameter growth starts after maximum temperatures reach 21°C. The seed normally ripens during August and September, with dispersal beginning immediately after ripening and continuing through to the following January. However, seed dispersal as early as July has been reported in Alaska. Opening of the mature female catkins is stimulated by low humidity and frost (Fowells 1965; Zasada 1971; Viereck and Little 1972; Marchant and Sherlock 1984).

REPRODUCTION

Seed Production and Dispersal: Paper birch trees begin bearing seed at about 15 years of age with the optimum bearing age between 40 to 70 years of age (Fowells 1965; Zasada 1971). Ripening occurs in late summer (early August to mid-September) and seed dispersal can occur as early as July 4, peaking between August and October (Zasada 1971). Seed production can range between 5.4 and 742 million seeds per hectare (Zasada 1977). Archibold (1980) estimated the seed rain for paper birch on burned areas to be 2.48 million seeds per hectare the 1st year and 1.03 million seeds per hectare the 2nd year, the numbers depending on the intensity of burning and hence the number of undamaged trees on the site, as well as the input from adjacent unburned areas. Seed production in a 76-year-old stand of paper birch was 89 million seeds per hectare (Bjorkbom *et al.* 1965). Good seed crops are produced every 2-4 years (Bjorkbom *et al.* 1965; Fowells 1965; Zasada 1971). The seeds of paper birch are small and lightweight and therefore dispersed by wind and water (Fowells 1965; Schopmeyer 1974). However, most seeds fall fairly close to the parent tree (Fowells 1965). In a burned mixed wood forest in northern Saskatchewan, the number of seeds on burned areas decreased with the distance from the unburned forest; the estimated dispersal distance on these sites was less than 100 m (Archibold 1980).

Seed Viability and Germination: While paper birch is a prolific seeder, seed viability is variable and decreases rapidly (Fowells 1965; Archibold 1980). In a burned mixed wood forest, 50% of seeds were viable on site the 1st year following burning, but only 16% were viable in the 2nd year. Zasada (1971) found an average seed viability of 17%, and estimated that 200-400 paper birch seeds were required to produce a single 1-year-old seedling. A study of seed pools beneath an undisturbed paper birch stand in New Brunswick found that the number of paper birch seeds was highest in the organic soil layers (4200-9400 seed/m^3) but no seeds were viable. Johnson (1975), studying seed pools beneath a number of subarctic forest stands, found buried seed in 65% of the stands sampled, with no relationship to either stand age or composition. No viable seeds were found. Seed may remain viable for up to 2 years only if the moisture content is low (Schopmeyer 1974). The percent of total germination and the number of days required to get 95% germination have been found to be higher during years with large seed crops than for years with poor seed crops. Seed germination is also related to seed weight, and increases as seed weight increases (Bjorkbom *et al.* 1965).

Exposure to a period of low temperature greatly improves germination rate (Nichols 1934). Paper birch seeds germinate in the spring following seed dispersal and tend to germinate following snowmelt, as soon as temperatures exceed a threshold value (Zasada *et al.* 1983). In Alaska, Zasada *et al.* (1983) believe differences in the timing of germination account for differences in survival. Germination is best where there is abundant soil moisture, shade, and freedom from excessively high soil temperatures (Marquis 1966; Horsley and Abbott 1970). It is best on exposed mineral soil since the presence of deep litter is not conducive to seedling establishment (Marquis *et al.* 1964; Marquis 1966; James and Courtin 1985). Tang and Kozlowski (1982) found that seeds germinate well in leaf litter, but die of desiccation if roots do not reach mineral soil. Thus, it appears that the best medium for germination is mineral soil, especially when mixed with organic materials, humus being a satisfactory medium and leaf litter a poor medium for germination. Germination of seeds is better on southern exposures than northern (Marquis *et al.* 1964) and germinants appear on south slopes earlier than on north ones (Zasada *et al.* 1983).

Vegetative Reproduction: In general, paper birch can regenerate from stump sprouts after cutting or fire (Fowells 1965; Hyvarinen 1968; Klinka and Scagel 1984, but see Zasada 1971; Foster and King 1986). Paper birch sprouts prolifically following cutting of young vigourous trees, but sprouting decreases with increased age of the tree (Fowells 1965). Dormant buds may sprout when an imbalance occurs between absorption of nutrients and actual nutrient requirements (Lust and Mohammady 1973). Sprouting may also occur at the base of standing live trees which become exposed when nearby trees are removed (Fowells 1965).

Paper birch can be propagated by cuttings, which are treated with a growth-promoting substance (Fowells 1965; Watson *et al.* 1980). Planting failure may be as high as 16% in the 1st month, with the most successful plantings usually occurring where the forest floor is removed (Bjorkbom 1972). While vegetative reproduction can be important for persistence of the species following disturbance, regeneration by seed is the most important means of reproduction for this species.

RANGE AND FORAGE VALUE

Paper birch is an important wildlife forage species, particularly for moose and deer (Jordan and Rushmore 1969).

PREDATION AND PESTS

Browsing by deer and moose may damage birch seedlings. Bjorkbom (1972) observed heavy moose damage where paper birch had been planted. Arlidge (1967) found that many 3-year-old paper birch seedlings had been browsed sufficiently by deer such that growth was checked. Small mammals can damage saplings by debarking to feed on the cambium (porcupine) or clipping off twigs and stems of seedlings (snowshoe hare). Mature trees may be susceptible to damage by yellow-bellied sapsuckers (Jordan and Rushmore 1969). Birds also feed on the buds, catkins, and seeds.

A large number of insect species will attack paper birch at all stages of growth and over all parts of the tree (Conklin 1969). Fowells (1965) and Conklin (1969) describe insect damage to paper birch in detail.

The most important diseases affecting paper birch usually result in discoloration and decay of the wood which is associated with mechanically caused wounds on low-vigour trees (Shigo 1969). A disease called "birch die-back" has been the subject of several studies in eastern North America. Trees die progressively from the top downward, the result being lowered vigour, reduced growth, and dying back of twigs and branches which may ultimately lead to the death of the tree (Fowells 1965; Hyvarinen 1968). A single factor causing birch dieback has not been determined, but those growing on thin soils with shallow rooting are more likely to develop this disease. This infers a possible climatic influence (Pomerleau and Lortie 1962). Fowells (1965) further describes the diseases of paper birch.

EFFECTS ON CROP TREES

Competition: When areas disturbed by harvesting and silvicultural practices are located near stands of mature trees, or where residual trees are left on-site to allow seeding-in, paper birch may inhibit coniferous regeneration (Gregory 1966).

Dense, vigourous stands of birch are considered to be a threat to the survival and development of spruce seedlings in the British Columbia Interior (Arlidge 1967). In Newfoundland, paper birch height will exceed that of balsam fir (*Abies balsamea*) by 73% on sites less than 10 years since disturbance, but 20 years after disturbance, paper birch is only 23% taller than balsam fir (Richardson 1979). Logan (1965) found that, when paper birch was competing with other hardwood species, leaf production and seedling growth were inhibited. In British Columbia, on sites where paper birch seeds-in densely or has sprouted from stumps, it competes with interior conifers.

Paper birch litter has been found to affect germination and early seedling growth of a number of plant species (Ahlgren and Ahlgren 1981). Germinants appeared later and total germination was significantly lower in paper birch litter compared to a control. White spruce seedling growth is significantly increased and mortality reduced if the seedlings are artificially protected against smothering and crushing by leaf litter: these factors reduce the establishment of white spruce beneath paper birch stands in Alaska (Gregory 1966).

Beneficial Effects: Few beneficial effects of paper birch on conifer growth are reported in the literature. A study conducted in the major forest types of interior Alaska found that paper birch forest floors had high total nitrogen and high organic matter content, and this was reflected in paper birch seedling yield (van Cleve *et al.* 1986). Paper birch has a relatively deep rooting habit, and a relatively high demand for soil nutrients. This, combined with the rapid turnover of deciduous foliage, may suggest that the soil organic matter content and associated levels of nutrients can be higher under birch than under a purely coniferous stand.

RESPONSE TO DISTURBANCE AND MANAGEMENT

Forest Canopy Removal: Where residual trees remain or where an adjacent seed source exists, abundant seeding-in of paper birch will normally occur following logging disturbance. However,

most seed is confined to within 100 m of standing trees (Archibold 1980) and felling of residual trees would greatly reduce the number of paper birch seedlings (Arlidge 1967). The sprouting vigour of mature trees cut during logging is variable (Fowells 1965) and may depend on the site condition. The size of "stools" (stumps and the new shoots developing from them) was much greater on protected woodland sites compared with those on drier ridge sites (James and Courtin 1985). Mortality of sprouts can be high (Fowells 1965).

Fire: Paper birch bark is thin and highly flammable, making it susceptible to fires of even moderate intensity (Fowells 1965; Foster and King 1986). Sprouting is common on trees that are damaged or killed by fire (Hosie 1973), but is more frequent in young stands than middle-aged to old stands. Organic soil stratigraphy of paper birch stands indicates that they are often the result of repeated episodes of conifer-dominated forest growth interrupted by fire (Foster and King 1986). Regeneration of paper birch is more frequent on burned areas than unburned areas (Behrend and Patric 1969). In Alaska, survival 3 years after burning was greater on high intensity burns than on moderate intensity burns (Zasada *et al.* 1983).

Cutting: Young, vigourous trees cut in the spring to stumps of 15-30 cm, sprout prolifically from either the root collar or the stump (Fowells 1965). Notch girdling or double-frill girdling may result in mortality or serious damage to trees.

Herbicides: Glyphosate provided excellent control of paper birch when applied in October as a foliar spray at rates of 2.24-13.42 kg a.i./ha in Ontario (Sutton 1978). Glyphosate (20% solution: 2 mL per 7.5 per cm dbh), hexazinone (pure: 2 mL per 7.5 cm dbh), and triclopyr (pure: 2 mL per 7.5 cm dbh) were effective in killing or seriously damaging paper birch trees when applied by hypohatchet in New Brunswick. Glyphosate was the most effective of the three herbicides. The spot gun and gridball techniques of hexazinone application were unsatisfactory in achieving objectives (Wile 1981). Triclopyr (full strength or half strength) was effective in controlling paper birch using the hack-and-squirt method of application in Maine. Hexazinone (full strength or half strength) caused severe defoliation using the same method (Filauro 1982). Triclopyr, tebuthiuron, and hexazinone (0-100 or 0-10 000 ppm) significantly reduced the germination and radicle growth of paper birch (Prasad 1983). Good control of paper birch was achieved with a foliar spray of 2,4-D ester at 3 kg a.i./ha in the Vancouver Forest Region. Spot application with hexazinone at 1.5 or 2.0 m spacing and 4 or 8 mL per spot, and broadcast application at 4.3 kg a.i./ha effectively controls paper birch (Expert Committee on Weeds 1985).

Insecticides: Paper birch seeds showed reduced germination following exposure to 10 ppm of the insecticide, fenitrothion, and marked toxicological damage when exposed to 1000 ppm (Weinberger *et al.* 1978).

Fertilizer: Paper birch responds very favourably to fertilization. Seedling height and biomass have been increased significantly with the addition of a N-P-K fertilizer (Bjorkbom 1973a, 1973b; Safford 1982; Bryant *et al.* 1987). Bjorkbom (1973a) reported a 19-fold increase in seedling height. Seedlings appear to be more responsive to changes in nitrogen than phosphorus and potassium. An increase in the potassium content of foliage was found with the addition of potassium, but no significant growth response occurred (Bjorkbom 1973b). Seedling response to fertilization has been favourable both under field and laboratory conditions (Safford 1982). Direct application of N and P dramatically increased the uptake of each of these elements by paper birch. Higher concentrations of elements were found in live branches of fertilized trees compared to those with unfertilized trees (Schmitt *et al.* 1981).

Fertilization of paper birch stands following thinning increased the diameter growth of remaining trees, the effect of which extended over a 10-year period (Safford and Czapowskyj 1986).

Soil Disturbance: Paper birch readily seeds into areas with soil disturbances caused by logging, slash burning and mechanical site preparation. Site scarification methods that expose mineral soil and/or mix organic and mineral soil layers provide the best seedbeds for paper birch (Marquis *et al.* 1964; Marquis 1966; Horsley and Abbott 1970). Seedling growth appears to be best where the sod is removed (Bjorkbom 1972). Stocking was 2-3 times greater on mechanically site-prepared areas than on areas that received no treatment (Bjorkbom 1967).

Other Environmental Disturbance: The response of paper birch to environmental stress is variable. Paper birch transition communities are widespread in the vicinity of pollution sources such as smelters. The species has been found to tolerate acid soils with elevated levels of Ni, Cu, and Al on woodland and ridge sites near Sudbury, Ontario. Sprouting of stumps after logging occurred on both woodland and ridge sites, but recruitment from seeds was low. It has been suggested that the influence of toxic metals in the soil leads to high metal:Ca ratios, which may lead to the induction of basal sprouts (James and Courtin 1985). Detrimental effects of SO_2 on paper birch have been reported. Sulphur dioxide causes partial stomatal closure, the formation of necrotic lesions on leaves, and an inhibition of the relative growth rates of roots and stems (Norby and Kozlowski 1983). Another study of germination responses to metal ions found no significant inhibition of germination in response to metal ions. Cadmium and lead were found to stimulate germination in relation to controls (Scherbatskoy *et al.* 1987).

Paper birch has been found to be sensitive to oil spills. Three years after an oil spill killed stands of paper birch, no sign of seedling establishment was observed (Hutchinson and Hellebust 1978 as cited in Watson *et al.* 1980).

Paper birch has the potential for use in mine reclamation in British Columbia and Alberta. It has been found to grow satisfactorily in the subalpine zone of southeastern British Columbia on coal mine spoils with low organic matter and high pH (6.5-8.5) (Watson *et al.* 1980).

Calamagrostis rubescens Buckl. — Pinegrass

DESCRIPTION

Pinegrass is a slender, tufted grass, with creeping rhizomes. It may produce moderate-sized clumps rather than single stems. It is 60-100 cm tall when flowering, but only 30-50 cm in the more common vegetative state. The stems have a reddish tinge at the base and a ring of hairs where the leaf meets the stem. The leaf blades are erect, 2-4 cm wide, flat or somewhat rolled, and are rough to the touch. The inflorescence (seedhead) is a congested, narrow panicle 7-15 cm long, pale or with a purplish tinge (McLean 1969; Hitchcock 1971; McLean 1979; Angove and Bancroft 1983). Pinegrass has rhizomes that grow mostly within the top 5 cm of mineral soil.

Variation: This species is found only in western North America, from southern British Columbia to California. There are no varieties or subspecies described in British Columbia (Taylor and MacBryde 1977).

DISTRIBUTION AND ABUNDANCE

Pinegrass is found throughout the central and southern interior of British Columbia. It is absent from the west side of the Coast Mountains and extends only as far north as Francois Lake and Fort St. James in the Interior. It is the most abundant grass in forested areas of the southern Interior. In the IDF and SBPS zones it is the dominant understory species, and it is common in drier subzones of the SBS and MS. It also occurs in drier subzones of the ICH and ESSF, and at low elevations and in moist areas of the PP and BG zones (McLean 1979; Angove and Bancroft 1983).

Altitudinal Range: Pinegrass ranges from the valley bottoms of the Interior to subalpine elevations. It is absent from the lower elevations of the PP and BG zones, but is found between 600 and 1850 m in the Similkameen Valley (McLean 1970).

HABITAT

Climatic Relations: The geographic distribution of pinegrass in the province suggests that it favours a continental climate with warm, dry summers, and can tolerate moderately cold, but not extreme, winter temperatures. It is not present in areas of high precipitation, and is absent from the hottest, semi-desert areas of the southern Interior. Tiedemann and Klock (1974) observed that it was most abundant on south aspects in Washington; Mueggler (1965) found no preference for aspect in northern Idaho.

Site and Soil Conditions: Pinegrass is found on a wide variety of well-drained sites within its geographic range. It grows on a wide variety of parent materials, slopes, and soils, but soils are most often well-drained, loamy to coarse-textured Luvisols and Brunisols (Freyman and van Ryswyk 1969; McLean 1970; Mitchell and Green 1981). Mueggler (1965) noted that pinegrass was frequently found on steeply sloping (>60%) sites with quartzite soils in the Cedar-Hemlock Zone of northern Idaho.

Nutrient Relations: In the SBS zone, pinegrass occurs on sites ranging from very low (oligotrophic) to moderately high (permesotrophic) nutrient regimes (Pojar *et al.* 1982). In southern British Columbia, it grows on a wide range of nutrient regimes from very poor to very rich (Mitchell and Green 1981). Soils supporting a heavy growth of pinegrass are frequently low in nitrogen, and increasing the levels of nitrogen, sulphur, or phosphorus may stimulate growth (Freyman and van Ryswyk 1969).

Water Relations: Throughout British Columbia, pinegrass often grows on soils that experience at least a moderate moisture deficit during the growing season. In the PP and BG zones, pinegrass occupies moister areas (McLean 1970). It is most abundant in the IDF zone, where it occupies extremely xeric to hygric sites (Angove and Bancroft 1983). The osmotic potential of pinegrass was found to

increase between mid-August and early September. This increase was thought to be due to the transport of solutes from the senesing leaves to perennating below-ground parts (Svejcar 1986).

Light Relations: Pinegrass is variously described as moderately shade-tolerant (Crane *et al.* 1983; McLean 1983) to very shade-intolerant (B. Mitchell, pers. comm., Nov. 1984). Throughout its range in British Columbia, it occurs in the understory of fairly open forests of pine, Douglas-fir, and aspen, but under these conditions it rarely flowers. In western Montana, it grows under dense canopies, but produces seed only in forest openings (Crane *et al.* 1983). Flowers and seeds are produced in open situations such as burns and clearcut areas (McLean 1979; Crane *et al.* 1983). McLean (1970) reported that between 600 and 900 m in the Similkameen Valley, pinegrass was present under Douglas-fir, but declined when stands were opened up. In the ESSF zone, however, between 1350 and 1850 m, pinegrass cover is most abundant in stand openings on south aspects.

In northern Idaho, pinegrass has been found to be less associated with canopy density than with shrub density, and is most frequently associated with dense shrub cover (60-90%) (Mueggler 1965).

Temperature Relations: No information is available.

GROWTH AND DEVELOPMENT

In the understory of forest stands, pinegrass forms a loose, open turf connected by a system of creeping rootstocks or rhizomes (McLean 1979). Fine fibrous roots are produced at each node of the rhizome (Hitchcock 1971). The rhizome and root system develops into a continuous dense mat, which tends to be shallow in depth (occurring in the first 5 cm of soil). This root system may establish more slowly than that of non-rhizomatous grass species such as orchardgrass (McLean 1969; Clark and McLean 1975).

Phenology: McLean and Tisdale (1960) reported collecting flowers of pinegrass on July 16 , early seed on August 5 , and late seed on September 2 near Kamloops. The leaves of pinegrass die in the early fall and new tillers are initiated each spring (Svejcar 1986). Pinegrass is available for grazing in the Kamloops and Cariboo Forest Regions between early May and late October (McLean *et al.* 1969).

REPRODUCTION

Seed Production and Dispersal: Pinegrass seldom produces seed except in forest openings or on recently burned or logged areas (McLean 1979; Crane *et al.* 1983). Seeds are in erect, spike-like panicles, and dispersal is primarily by wind (Hitchcock 1971). Following a wildfire in western Montana, pinegrass bloomed profusely the first postfire growing season and in the succeeding 3 years (Crane *et al.* 1983). In northern Idaho, pinegrass produced seeds during the first decade following a wildfire (Stickney 1986).

Seed Viability and Germination: McLean (1967) found maximum germination of pinegrass to be 38%. Neither stratification nor scarification of the seed is necessary to induce germination. The lack of a chilling requirement suggests that pinegrass may germinate in the fall or whenever an adequate supply of moisture is available (Grime 1981).

Vegetative Reproduction: Pinegrass establishes and regenerates primarily through the lateral extension of creeping rhizomes (McLean 1979; Crane *et al.* 1983), forming thick rhizome sods (Svejcar 1986). Following wildfire in northern Idaho, pinegrass reproduced both vegetatively and by seed (Stickney 1986).

RANGE AND FORAGE VALUES

Pinegrass is an important species for summer grazing throughout south and central British Columbia (McLean 1979), and may provide approximately 50% of the forage by weight (Freyman 1970). It is given a low to medium preference by grazing livestock in the spring and its forage value declines over the growing season (McLean 1970). Pinegrass has a medium-level nutritive value for crude protein in early

summer, declining thereafter, and a medium-level nutritive value for crude fibre in early summer, increasing towards the fall (McLean and Tisdale 1960; Johnston and Bezeau 1962; Freyman 1970; McLean 1979). Phosphorus decreases and calcium increases with maturity (McLean and Tisdale 1960; Johnston and Bezeau 1962). In general, the palatability of pinegrass decreases over the growing season and this seasonal decline is reflected in a decline in the daily average weight gain of cattle (Johnston and Bezeau 1962; McLean 1979). Trace element content analysis of pinegrass shows that copper and molybdenum levels are satisfactory for livestock over most of the growing season, whereas zinc is below the minimum requirements for livestock (Fletcher and Brink 1969). It has been noted that pinegrass is often more nutritive when growing in forest openings and on burned areas under full sunlight, than when growing in the shaded forest (McLean and Tisdale 1960; McLean 1979).

EFFECTS ON CROP TREES

Competition: Pinegrass is a major competitor with crop trees in the south and central interior of British Columbia, particularly in the IDF zone. While it is generally agreed that grass competes with conifer regeneration, the degree and causes are poorly understood. Competition is usually most severe on droughty sites, so that competition for moisture appears to be the dominant mode of competition. Competition for soil nutrients also occurs, and the degree of competition between pinegrass and tree seedlings may be influenced by soil fertility (Clark and McLean 1975). Shading and smothering by pinegrass appear to be of relatively minor importance.

Tree seedlings that have not yet established a good interlocking root system compete poorly with grass for available moisture. Seedlings that are established before grass invasion have a good chance of survival, whereas those established simultaneously with, or later than, the grass may grow poorly. An experiment by Clark and McLean (1975) suggested that pinegrass provided less competition to lodgepole pine than orchardgrass (a commonly seeded, non-rhizomatous forage species) because pinegrass was slower to develop its root system.

Beneficial Effects: There are several possible beneficial effects of pinegrass growing in association with coniferous trees. The rhizomatous growth habit and the dense network of fine roots provide excellent control of surface soil erosion. A cover of grass incorporates valuable, nutrient-rich organic matter into surface soil layers. Pinegrass may also play a role in excluding invasion of more competitive species; and Clark and McLean (1975) suggested that a cover of pinegrass might help to reduce or prevent overstocking of lodgepole pine.

RESPONSE TO DISTURBANCE AND MANAGEMENT

Forest Canopy Removal: In the Similkameen Valley, pinegrass decreases in abundance following logging of low-elevation, open, Douglas-fir-fescue ecosystems, but increases following canopy removal in the Douglas-fir-pinegrass type and in subalpine fir forests (McLean 1970; McLean *et al.* 1971). This difference in response according to elevation may reflect the relative moisture and temperature stresses that the plant experiences following canopy removal. In the northern Rocky Mountains, pinegrass was much less abundant on logged and logged and grazed sites (Cholewa and Johnson 1983). Thinning of dense ponderosa pine produced over a 40% increase in pinegrass cover in eastern Washington where spacings were greater than 5.5 m. No increase was noted on the 4.0 m spacings (McConnell and Smith 1970).

Fire: Fires of light to moderate intensity create a favourable post-fire environment for pinegrass development (Stickney 1981). In western Montana, pinegrass abundance increased until the 5th year following a fire, reaching a stable level of cover which was well above the preburn level for at least 10 years (Stickney 1981, 1986). In the cedar-hemlock forests of northern Idaho, pinegrass was most abundant on sites that had experienced multiple burns over a 30-year period (Mueggler 1965). Pinegrass is considered to be a fire "survivor" (Stickney 1986), sprouting profusely after fire (Tiedemann and Klock 1974). Its roots and rhizomes are found within the upper 5 cm of soil, so any fire that penetrates the duff layer can be expected to do extensive damage (McLean 1969). It is common for pinegrass to produce seed for the initial years following fire.

Cutting and Grazing: Pinegrass is susceptible to heavy grazing. Clumps may be removed easily, recolonized in part by other species (McLean 1979,1983; Cholewa and Johnson 1983). Environmental conditions, especially summer rainfall, affect the response of the species to grazing or clipping, and year to year fluctuations in growth because of environmental variability can exceed variation from grazing treatments (Stout *et al.* 1981). Pinegrass failed to regrow when clipped in mid-July because of the depletion of surface water supplies (Freyman and van Ryswyk 1969). Stout *et al.* (1981) clipped pinegrass throughout the summer at three intensities for 4 consecutive years . Clipping to 15 cm did not significantly affect stand vigour, but the 5-cm and 10-cm clipping treatments resulted in a steady decline in plant yield. The largest decrease in production occurred after the 1st year of treatment, and the plants were most sensitive to foliage removal in early July.

After 6 years without clipping, pinegrass had not recovered (Hall *et al.* 1987). Modelling has shown three stages of pinegrass recovery: (1) a lag of 1 year, followed by (2) a period of exponential increase, with (3) a subsequent levelling off. The model predicted that clipping for 4 consecutive years to a stubble height of 5 cm would require a recovery period of 20 years after clipping ceases (Hall *et al.* 1987). Stout and Brooke (1987) have conducted studies that compare the effects of clipping versus grazing on pinegrass yield and tiller production. Grazing and clipping were found to have similar effects on yield in the subsequent year. However, grazing involved the removal of plant parts or the pulling out of entire tillers with roots. It tended to stimulate new tiller production, whereas clipping did not.

Herbicides: Hexazinone applied at 2.2 kg/ha as either a pre- or post-planting treatment provided good to excellent control of pinegrass for two growing seasons (Dimock *et al.* 1983). Other chemicals show mixed results (Stewart and Beebe 1974; Dimock *et al.* 1983). Dalapon® and Atrazine® both provided intermediate (50-75%) kill of pinegrass with an increased survival of ponderosa pine seedlings (Stewart and Beebe 1974). Roundup®, Atrazine® and Dalapon®, Dalapon®, and Velpar® applied by foliar spray at various rates severely injured or killed pinegrass (Boyd *et al.* 1985). Stewart and Beebe (1974) found that the mulch of dead grass present after spraying may have aided survival of planted conifers by conserving soil moisture and reducing high surface soil temperatures.

Soil Disturbance: Anchor chain drag scarification has been shown to increase the cover of pinegrass significantly on some clearcut areas in British Columbia. Light to medium soil disturbance favours pinegrass, but heavy soil disturbance may cause a reduction in cover. Patch scarification was less effective than herbicides in controlling competition by pinegrass and other seeded grasses in central Washington (Stewart and Beebe 1974).

Fertilization: Freyman and van Ryswyk (1969) tested response of pinegrass to 100-200 kg/ha of ammonium nitrate, phosphorus, potassium, and sulphur. Nitrogen significantly increased growth and yield of pinegrass on all sites. Nitrogen combined with low levels of sulphur stimulate the most vigourous growth, but high rates of sulphur caused some mortality of pinegrass. Fourteen percent of the applied nitrogen was recovered by pinegrass; 23% was recovered when sulphur was also applied. Phosphorus at 200 kg/ha, in combination with other nutrients, increased yields significantly. McLean (1979) reports an increase in protein levels from 8.5 to 17.0%, and a doubling of forage yields with the application of nitrogen and sulphur. Heavier rates of nitrogen lead to effects that lasted from 3-5 years. Response to fertilizer applied in mid-July was poor because soil moisture was not sufficient for absorption of nitrogen. Grasses take up nutrients better than conifers. Thus, applications of fertilizer may have a detrimental effect on planted conifers because of the increased competition from vigourous pinegrass.

Epilobium angustifolium L. — Fireweed

(*Chamaenerion angustifolium*)

DESCRIPTION

Fireweed is a tall herbaceous perennial that forms extensive colonies through a spreading system of fleshy roots or "pseudorhizomes." The root system gives rise to erect, usually unbranched annual shoots 1-3 m tall. The untoothed, linear to lanceolate leaves are spirally arranged around the stem. Each stem has a large, showy terminal cluster of pink to purple or occasionally white flowers. The fruit is a narrow capsule, up to 10 cm long, that releases large numbers of plumed seed (Lyons 1952; Hitchcock *et al.* 1961; Mosquin 1966; Hulten 1968; Clark 1976; Myerscough 1980).

Variation: Epilobium angustifolium is a completely circumpolar species with two recognized subspecies (Myerscough 1980). Both subspecies occur in British Columbia. The ssp. *angustifolium* is found in the northern boreal forests and at high elevations in the mountains, while ssp. *circumvagum* occurs at lower elevations in south and central British Columbia. The latter subspecies has larger leaves and is generally taller and coarser than ssp. *angustifolium*. There is considerable intergradation where these two subspecies overlap (Mosquin 1966).

DISTRIBUTION AND ABUNDANCE

Fireweed is found throughout British Columbia, and occurs in all biogeoclimatic zones wherever soil moisture is sufficient (McLean 1979). It is extremely common and abundant throughout the central and northern Interior, but is less abundant on the outer Coast and in the dry Southern Interior (Angove and Bancroft 1983).

Altitudinal Range: In British Columbia, fireweed ranges from sea level to high alpine meadows. It has been found at elevations as high as 4000 m in the mountains of western North America (Mosquin 1966).

HABITAT

Climatic Relations: The extremely broad range of this species indicates that it can tolerate a wide range of climatic extremes. In northern climates it appears to be confined to warm sunny locales and south-facing slopes. Towards the central portion of its range, including British Columbia, it occurs on a wide range of slopes and aspects. In hot, dry climates at the southern end of its distribution, it favours cool, moist, shaded locales, and high alpine and subalpine habitats (Myerscough 1980). Mosquin (1966) indicates that the plants are frequently sterile at the northern limits of its range in Canada.

Site and Soil Conditions: Fireweed tolerates a very wide variety of soil and site conditions (see, e.g., Myerscough 1980 for Britain), but is most commonly associated with disturbed sites such as logged, windthrown, or slashburned areas (Dyrness 1965; McLean 1979), recently deglaciated terrain, or mine wastes (Kimber *et al.* 1978; Watson *et al.* 1980).

Epilobium angustifolium also occurs in mature forests in the Interior of British Columbia (see, e.g., Pojar *et al.* 1984), and is common in undisturbed alpine and subalpine meadows (Mosquin 1966). It is also a major component of plant communities growing in avalanche tracks in the western Cascades (Douglas 1972). It occurs on organic soils, but also on soils with little or no organic matter. It is found on virtually every kind of parent material, and on a wide range of soil textures, but is most common on sandy loam to loamy soils (Myerscough 1980).

Water Relations: Myerscough (1980) reports that *E. angustifolium* occurs most commonly on soils that are at least freely drained, but that it occasionally occurs in waterlogged mires. Fireweed is reported to be intolerant of waterlogging (Etherington 1983, 1984). It tolerates a wide range of moisture conditions (Angove 1981; Pojar *et al.* 1982; Angove and Bancroft 1983), but grows most vigourously on subhygric to hygric seepage sites (Brand 1984 in Haeussler and Coates 1986).

Towards the northern limits of its range it may become less tolerant of excessive moisture and may be restricted to well-drained soils (Myerscough 1980). Although it tolerates rather dry sites, it does not germinate under droughty conditions (Watson *et al.* 1980). Fireweed plants tolerate drought by maintaining a consistently slow rate of transpiration (Nazrul-Islam 1983).

Light Relations: Fireweed grows most often on open ground, and is light-demanding (Watson *et al.* 1980). Flower buds form earlier in unshaded colonies than in shaded ones and in deep shade the plant does not flower (Myerscough 1980). In intermediate shade and full sun, plants have roughly equivalent growth rates, but in deep shade growth rates are much reduced and seedlings are etiolated (Myerscough and Whitehead 1967; Morgan and Smith 1979).

Temperature Relations: The range of this species suggests that it is adapted to survive and grow under a variety of temperature regimes. Under experimental conditions, roots initiated growth at 4.5°C, while shoot growth occurred only at higher temperatures (Myerscough 1980). Emergent shoots tolerate some frost in spring but may later show minor tissue damage.

GROWTH AND DEVELOPMENT

Under favourable environmental conditions, fireweed seedlings grow at a comparatively rapid rate for the first 5 weeks from seed. Seedlings that germinate in late summer or early fall occasionally overwinter as a small rosette of evergreen leaves, but spring germinants may reach a mature height and produce flowers during their 1st year of growth (Myerscough 1980).

The seedling quickly develops an extensive root system. Shoot buds are produced along the length of the root system, giving rise to a colony of plants. These shoots expand late in the growing season and overwinter just beneath the soil surface (Myerscough 1980). In the spring, they emerge from the soil to form erect annual shoots. Aerial shoots normally exceed 1 m in height at maturity, but height growth seems to be strongly correlated to environmental conditions, and best growth is generally observed on moist, subhygric sites under full light conditions. Up to 120 shoots per square metre have been observed in some populations, and emergent shoots may reach a maximum biomass of 600-900 g/m^2 (van Andel 1975).

Myerscough (1980) states that the fleshy underground roots of fireweed are most abundant at 5-20 cm below the soil surface and can penetrate deeper than 40 cm. This does not appear to be the case in southern British Columbia, however, where McLean (1969) found most roots located between 1.5 and 5 cm beneath the soil surface. Lateral spread of a colony of fireweed averaged 1 m per year in one direction (van Andel 1975). Growth "fronts" result in a clumped distribution of fireweed during invasion. As a site becomes fully occupied, this clumped distribution declines as a result of competition between individual stems (Ford and Renshaw 1984). There is no information about how large a colony can become, but field populations have a longevity of several decades, and the roots can live for over 20 years (Moss 1936; van Andel 1975).

The development of a population of *E. angustifolium* along a roadside in Britain was studied for 20 years (Myerscough 1980). There was a progressive increase in aboveground biomass of the colony for the first 7 years, with the population remaining fairly stable for 12 years, followed by a rapid decline in biomass as die-back occurred. Development of fireweed stands may be quite different in may areas of British Columbia because succession proceeds too rapidly to allow pioneer conditions favourable to fireweed to persist for as long as 20 years. In the CWHa subzone, for example, fireweed appears to reach its peak dominance in the second or third growing seasons following disturbance, and subsequent in-growth of shrubs and trees is rapid. Once a forest canopy develops, fireweed generally dies out, but it can persist in the understory of open stands in the British Columbia Interior (Mosquin 1966).

Phenology: Roots begin growing before shoot buds below the surface begin to elongate. Aerial shoots first begin to emerge anywhere from late March to early June at mid-latitudes, but most emerge in May. Leaves are full grown approximately 1 month later and maximum biomass is reached between the middle of June and the end of August. Aerial shoots begin to wither in late July or early August and all have died back by late September or early October (Myerscough 1980; Schmidt and Lotan 1980). At mid- to high-elevations, communities may not reach their maximum height until mid-summer (Douglas 1972).

The flowering season extends from June to September because the inflorescence begins to flower at the base and continues to elongate during the summer, producing blossoms at the tip of the plant long after the basal fruits have ripened and released their seed (Clark 1976). In the intermountain U.S., seed ripening begins in late July (Schmidt and Lotan 1980). Seeds are released throughout the late summer until after the aerial shoots have withered in autumn.

REPRODUCTION

Seed Production and Dispersal: The plants can flower in their 1st year of growth from seed. The flowers are nectar producers and are thus sought out by bees, butterflies, and other insects. Production of seeds is usually copious in temperate environments. There are an estimated 250-500 seeds in each capsule, and estimates of production for each live stem range from 20 000 to 80 000 or higher. The plumed seeds are dispersed by the wind, and they are very slow to settle (Salisbury 1961; Myerscough and Whitehead 1965; Mosquin 1966; Myerscough 1980; MacNaeidhe and Curran 1982). Fireweed accounted for 63% of the seed obtained in seed traps 1 year after fire at a northern Saskatchewan site (Archibold 1980). This represented 5.66 million seeds per hectare.

At the northern limits of its range, fireweed may not produce ripe seeds regularly (Mosquin 1966; Myerscough 1980; Fredskild 1984).

Seed Viability and Germination: Most fireweed seeds germinate during the 1st year (Granstrom 1987). Seed may remain viable for up to 2 years, but normally loses much of its viability after 18 months (Myerscough 1980). Germination is stimulated by light, a chilling period, and treatment of seed with dilute acid (Myerscough and Whitehead 1965; McLean 1967; Myerscough 1980).

Seed may germinate during late summer or early autumn, or during the following spring. Optimal temperatures for germination are between 15 and 35°C (Myerscough 1980). Only seeds at or near the soil surface will germinate (Myerscough and Whitehead 1965). Germination is most successful on moist, open sites that have few initial plant competitors (van Andel and Rozema 1974). Increased nutrient availability may improve germination in laboratory experiments (Myerscough and Whitehead 1965). However, field experiments have not shown improved germination following nitrogen fertilization of established communities, because of the competition for water in these communities (van Andel and Rozema 1974). Fireweed seed does not germinate under dry soil conditions (Myerscough and Whitehead 1965). Oberbauer and Miller (1982) found that no germination occurred when soil water potentials were below -3 bars. Seed germination may also be reduced by leachates from conifer leaves and litter (Jobidan 1986).

Archibold (1980) found viable buried seed in soil cores taken immediately following a fire in northern Saskatchewan. He speculates that seed banking may account for the rapid invasion of fireweed on burned sites. However, given the short viability of fireweed seed, it does not seem likely that large quantities of viable seed could accumulate in the forest floor at a depth sufficient to survive a forest fire.

Vegetative Reproduction: Fireweed relies on large quantities of seed to colonize disturbed areas, but once it arrives on a site, the population expands by vegetative reproduction. New shoots arise each year from buds located at the base of old stems, and on the horizontally spreading root system 2-8 cm below the soil surface. The root system is perennial: it spreads further outward from the original seedling each year. New plants are created when they become detached from the parent plant through death of old roots or through disturbance. In an established colony of fireweed, vegetative reproduction has priority over reproduction by seed (Moss 1936; van Andel and Rozema 1974; Myerscough 1980).

RANGE AND FORAGE VALUE

Fireweed is grazed by cattle, elk, deer, and moose (McLean 1979; Watson *et al.* 1980). Grazing occurs throughout the growing season, but particularly when plants are in flower (McLean 1979).

PREDATION AND PESTS

Small mammals use fireweed seed (Watson *et al.* 1980). Myerscough (1980) provides a comprehensive list of the many insects and diseases found on *E. angustifolium* in Britain.

EFFECTS ON CROP TREES

Competition: Fireweed is generally considered to be a species of low competitive ability because it is a pioneer of recently disturbed sites and does not invade sites with established vegetation cover (Mosquin 1966; Watson *et al.* 1980). However, dense fireweed communities may interfere with the survival and growth of conifer seedlings.

Fireweed is more of a concern in central and northern parts of British Columbia than on the coast because: 1) slower-growing seedlings may be overtopped by fireweed for 10 or more years following establishment, 2) fireweed communities persist for more than a decade, and 3) growing seasons are shorter. Fireweed may physically damage conifer seedlings by press from dead shoots. Douglas-fir and western larch seedlings appear to be particularly susceptible to this type of damage because young seedlings are very flexible and lacking in caliper. Increased susceptibility may result from stem elongation in response to reduced light levels beneath dense fireweed canopies. Physical damage from fireweed appears to be greatest where fireweed cover is dense, plants are tall, and rainfall and snowfall are high.

Dense canopies of fireweed may cause substantial reductions in the amount of light received by overtopped conifer seedlings. Light regimes below 5% of full sunlight have been recorded in dense patches of fireweed.

Aerial shoots and foliage grow up from the ground each spring and develop to maximum cover and height within approximately 1.5 months. Because of the lack of perennial aboveground stems, trees are free of competition for light during early spring. In coastal areas, conifer seedlings may be able to achieve substantial photosynthesis during the winter, when fireweed is leafless. This may reduce the impact of fireweed cover on seedling growth.

Competition between fireweed and conifers for moisture and nutrients has not been demonstrated in British Columbia. However, it may be important under some conditions. Fireweed grows vigourously and may tie up nutrients in its root systems and in aboveground biomass. This may limit availability of nutrients, such as nitrogen and phosphorus (van Andel and Nelissen 1979).

Beneficial Effects: Fireweed may delay development of shrubby vegetation on cleared or burned areas (see, e.g., Stickney 1981), thus allowing planted conifers to gain dominance of a site when they outgrow the fireweed. Its extensive root system helps to bind soil and reduce erosion (Watson *et al.* 1980). Invasion by fireweed undoubtedly increases the organic matter content and probably the nutrient capital of severely burned or otherwise disturbed sites.

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: Fireweed aggressively colonizes logged-over areas (Mosquin 1966). Colonization is achieved primarily by seeding-in, but where fireweed already exists before canopy removal, it is able to expand by means of its spreading root system (McLean 1979; Myerscough 1980; Rowe 1983).

In Eis' (1981) study of four SBS site types north of Prince George, fireweed was absent from all sites before logging. He observed that the "first few seeds arrive in the fall of the first year following winter logging and germinate in the spring of the second year. Its presence is most noticeable during the third year after logging and ... it appears in great numbers during the fourth year." Six years after logging, fireweed accounted for greater than 60% of the herbaceous ground cover on the Cornus-Moss type and 50% on the Dryopteris-Aralia type, but was less than 20% of the cover on the Devil's club site and was not a significant competitor on the Alluvium site. This study demonstrates that fireweed is able to rapidly exploit a vacant niche but is unable to compete where vegetation is already well established. The Cornus-Moss type had a low diversity and cover of vegetation immediately after logging and fireweed readily became dominant. In contrast, shrubs

and herbs were already well established on the Alluvium site and fireweed was unable to move in. Maximum cover of fireweed is usually achieved within 3-5 years of harvesting (Isaac 1940).

Fire: Fireweed is well known in western North America for its ability to invade recently burned areas (Mosquin 1966; Dyrness 1973; Watson *et al.* 1980; Stickney 1981; Cholewa and Johnson 1983; Stickney 1985; Foster 1986). Its light, wind-dispersed seeds rapidly colonize vacant ground created by burning. Following fire it can form uniform stands over vast areas. Cover, density, and production of fireweed are usually greatest on areas that suffer most intense burns (Ahlgren 1960; Mueggler 1965; Morris 1970; Bartos and Mueggler 1981; Dyrness and Norum 1983).

Maximum fireweed cover is generally reached 2-3 years after burning and may then either decline or remain static (Kellman 1969; Miller and Miller 1974; Tiedemann and Klock 1974; Bartos and Mueggler 1981; Stickney 1981, 1986). The longevity of fireweed dominance of seral communities depends on the rate of development of other herb and shrub species (Stickney 1986).

McLean (1969) classified fireweed as moderately susceptible to fire because its fibrous roots are mostly located within the upper 5 cm of the mineral soil. Where it is more deeply rooted, it is more tolerant of fire. Fireweed rapidly loses vigour and will not survive under regimes of frequent burning (Myerscough 1980); however, it has a very low flammability and can suppress fire in early successional vegetation where it is abundant. The plant acts as a heat sink because of its high moisture content and there is little standing dead fuel because its litter decomposes rapidly (Sylvester and Wein 1981).

Cutting and Grazing: There are no reports in the literature describing the response of fireweed to manual cutting. Impact is expected to be short-lived and minimal unless cutting is repeated within short periods of time. Fireweed does not survive continued grazing (Myerscough 1980; Coates and Haeussler 1986).

Herbicides: Bailey and Hoogland (1984) describe the results of laboratory experiments with several herbicides on *E. angustifolium*. Soil-acting compounds which were found to kill fireweed included: bromacil, cyanazine, ethofusemate, lenucil, oxadiazon, oxyfluorfen, propyzamide, propachlor, and simazine. Foliar applications of 2,4-D amine, mecoprop, triclopyr ester, paraquat, and pentachlor + chlorprophan have been found to give effective control of fireweed (Turner and Richardson 1979; Bailey and Hoogland 1984). Glyphosate is reported to give short-term reductions in cover although it does not immediately kill fireweed (Blackmore and Corns 1979; Bailey and Hoogland 1984; Expert Committee on Weeds 1984; Hann 1986). In a study near Prince George, foliar application of glyphosate, at 2.25 kg/ha in early August, significantly reduced height of fireweed two growing seasons after treatment, but did not significantly reduce percent cover (Expert Committee on Weeds 1985). Treatments with herbicides such as dalapon, glyphosate, and hexazinone (granular and liquid broadcast) do not usually cause significant reductions in fireweed cover (Expert Committee on Weeds 1985, 1987).

Sulfometuron methyl (Oust®) effectively controls fireweed when applied at 600 g a.i./ha in August (Expert Committee on Weeds 1986).

Soil Disturbance: Fireweed is known to rapidly invade exposed mineral soil and peat (Wein and Bliss 1973; Watson *et al.* 1980; Conn and DeLapp 1983), and it is widespread on roadcuts throughout central and northern British Columbia. In the Gaspé Region of Quebec, Mosquin (1966) observed that fireweed was growing poorly on exposed subsoil, but had very good vigour on adjacent sidecast mounds of humus and topsoil.

Fertilization: Fireweed may increase in abundance where fertilizers have been used in silviculture (Reinikainen 1964 as cited in Myerscough 1980). Germination is improved on fertilized sites lacking vegetation cover (Myerscough and Whitehead 1967). However, when plant cover is well established, fertilization may not increase germination of fireweed (van Andel and Rozema 1974).

Other: Areas seeded to grass can have lower cover and frequency of fireweed than unseeded areas (Hernandez 1973 as cited in Watson *et al.* 1980; Crane *et al.* 1983).

Menziesia ferruginea Sm. — False azalea

(rusty menziesia, Pacific menziesia)

DESCRIPTION

False azalea is an erect shrub up to 2 m tall with finely pubescent young twigs and smooth or loosely shedding bark on older branches. Leaves are alternate, thin, light or bluish-green, oblong to obovate, slightly toothed along margins, and up to 6 cm in length. Flowers are yellowish, tinged with red (appearing pinkish), up to 1 cm long and cylindric-urceolate in shape. They are borne in terminal clusters on the previous year's shoots. The fruit is a thin-walled, ovoid, septicidal capsule up to 8 mm long, which dehisces at maturity (Szczawinski 1962).

Variation: Two subspecies of *Menziesia ferruginea* have been identified in British Columbia, subspecies *ferruginea* along the coast and central Interior, and subspecies *glabella* in the southeast (Szczawinski 1962). However, Hickman and Johnson (1969) concluded from a study of morphological variation in false azalea in northwestern North America that, although significant and complex patterns of variation occurred among individuals, there was no basis for the construction of subspecific taxa. They proposed that *M. ferruginea* var. *glabella* be considered a synonym for *M. ferruginea*. For the purposes of this synopsis, *M. glabella* is considered synonymous with *M. ferruginea*, but the authors' original terminology is retained.

DISTRIBUTION AND ABUNDANCE

False azalea occurs in coastal and mountainous regions throughout the province. It has been collected at localities all along the coast, on the west side of the Coast Mountains (Klinka *et al.* 1982; Haeussler *et al.* 1984) and in the Interior Wet Belt. Few specimens have been collected from the Interior Plateau and parts of the northern Interior (Lloyd 1984; Caza and Kimmins 1987). It has not been reported from northeastern British Columbia. East of the Coast Mountains, it occurs mainly above 900 m. Outside the province, false azalea occurs north along the Alaska coast and south along the Pacific coast to California, inland across the Cascades and Rocky Mountains to Wyoming (Szczawinski 1962; Hickman and Johnson 1969). It is common from sea level to alpine tundra along British Columbia's coast and occurs in all biogeoclimatic zones but the IDF, PP, BG, SBPS, BWBS, and SWB .

Vegetation Associations: False azalea is abundant in only the CWH, MH, ESSF, and CCPH zones. Klinka *et al.* (1982) classified false azalea as a differentiating species in the CWHd *Thuja plicata-Abies amabilis/Athyrium (filix femina) - Oplopanax (horridus)* (Upper Montane) subassociation in southwestern British Columbia. This ecosystem is the most productive for *Picea engelmannii* in the region. Associated species included *Orthilia secunda*, *Rubus pedatus*, *Rhytidiopsis robusta*, and several *Vaccinium* species. Haeussler *et al.* (1984) also found false azalea to be a major species in many associations of the $CWHf1_1$ and $CWHf1_2$ in the Prince Rupert region on xeric to subhygric and poor to rich sites. Associated species were *Tsuga heterophylla, A. amabilis, T. plicata, Picea* sp., *Vaccinium* spp., *R. pedatus*, and *Cornus canadensis*. Haeussler *et al.* (1985) identified false azalea as an important component of associations in the ICHg, the northwestern transitional subzone in the Prince Rupert region. It is a common species in parts of the ICHw and ICHv in the North Thompson-Shuswap drainage (Lloyd 1984) where it occurs on xeric to subhydric sites with *T. heterophylla, T. plicata, Vaccinium* spp., *C. canadensis* and *Ptilium crista-castrensis*. Peterson (1965) and Brooke *et al.* (1970) found false azalea to be a constant dominant and a differentiating species in several associations on mesic sites in the coastal subalpine MH zone.

False azalea also occurs with less abundance in moderately dry lithic habitats, and hygric habitats with deep soils and temporary seepage in this zone. It is a characteristic species of the ESSFf in Western Kamloops Region (Mitchell and Green 1981) and the ESSFm and ESSFw in the North Thompson-Shuswap drainage basin (Lloyd 1984; Caza and Kimmins 1987) in the Interior. It can be found on all hygrotopes in these subzones.

HABITAT

Climatic Relations: False azalea is found predominantly in ecosystems with abundant moisture. It is absent from the drier biogeoclimatic zones in the province. Discontinuities in its distribution in British Columbia (for example, the central Interior) may be due to climatic moisture constraints, or may have a historical explanation (Hickman and Johnson 1969). Similarly, its absence from northeastern British Columbia implies that its distribution may be limited by cold temperatures. Like *Rhododendron albiflorum*, false azalea may be restricted to areas with adequate snow cover, which protects plants from winter desiccation (see *R. albiflorum* synopsis).

Site and Soil Conditions: False azalea is most well developed in mesic habitats, but can occur on a wide variety of sites. Brooke (1965) found false azalea to be a differentiating species on sites in the MH, characterized by glacial till materials, all slope positions and exposures, elevations above 1050 m, snow 7 months of the year, and Mor humus forms. Lowdermilk (1925) found *M. glabella* on sites in spruce-fir forests, ranging from lower slope, southwest exposures with little vegetation cover to upper slope, northeast exposures with very dense shrub covers. Mueggler (1965) found *M. glabella* to be positively associated with sites of northern exposure in cedar-hemlock stands in northern Idaho. False azalea occurs on shallow rocky soils and deep wet soils and in bogs (Hickman and Johnson 1969; Brooke *et al.* 1970). Soils on which false azalea is typically found are predominantly Humo-Ferric or Ferro-Humic Podzols with a Mor humus.

Nutrient Relations: False azalea is typically found on sites with low pH. Brooke *et al.* (1970) cite pH values of 3.5-4.5 for sites in the MH, Lloyd (1984) gives 4.5 for the interior ESSF, and Haeussler *et al.* (1984) give values of 3.0-4.5 for associations with false azalea in the Prince Rupert CWHf. Across the zones in which it occurs in British Columbia, it can be found on very poor to very rich sites (Brooke *et al.* 1970; Klinka *et al.* 1982; Haeussler *et al.* 1984). However, Mueggler (1965) found the distribution of *M. glabella* in cedar-hemlock stands to be positively associated with low K content of soil and a high organic matter content (5.6-8%). Economou and Read (1986) demonstrated that hardy deciduous Azalea species grew best at pH 4.0.

Water Relations: No specific information is available on the water relations of this species. Where climatic moisture is abundant, false azalea occurs on mesic sites that are well to moderately drained (Mitchell and Green 1981). The species can occur on xeric sites, where there is sufficient precipitation (Haeussler *et al.* 1984), but has also been reported in poorly drained coastal bogs (Hickman and Johnson 1969).

Light Relations: False azalea can persist in heavily shaded forests where light levels are typically 5% of full sunlight, suggesting that the species is very shade-tolerant. Similarly, Mueggler (1965) found that the relative importance of *M. glabella* increased as the canopy closed in cedar-hemlock forests in Idaho. Alaback (1982), however, reported decreases in false azalea biomass in spruce-hemlock forests in Alaska, over 30 years of age. The shrub biomass was lowest in stands from 31 to 130 years, when forest overstory productivity was highest. After this period, false azalea biomass increased again to approximately 20% of the value in the young forest. The best development of individuals appears to occur in the partially shaded conditions of openings among the tree clumps characteristic of the mature subalpine forests of the ESSF and MH (Brooke *et al.* 1970; Caza and Kimmins 1987).

Temperature Relations: No information is available.

GROWTH AND DEVELOPMENT

False azalea has an open, branching growth habit and does not form dense canopies, because of its small leaf size. Maximum height of plants at maturity may reach 3 m, but 2 m is typical. Mueggler (1965) found that maximum heights of false azalea in both disturbed and undisturbed stands of cedar and hemlock in Idaho was 1.2 m. The longevity of false azalea plants is not known, but other co-occurring ericaeous species may live over 100 years (see *R. albiflorum* synopsis). Alaback's (1982) study indicates plants survive at least 30 years in northern forests.

Phenology: In northern and subalpine forests, false azalea flowers from late May through July. Leaves expand rapidly in early June at the time flowers open, and begin to senesce in mid-August and September at high elevations in southern British Columbia (C. Caza, pers. obs., 1987). Capsules mature and open in late August or early September at high elevations.

REPRODUCTION

Seed Production and Dispersal: Numerous, small seeds are produced in capsules which dehisce naturally at maturity (Szczawinski 1962). Seed is wind- or gravity-dispersed.

Seed Viability and Germination: No information is available.

Vegetative Reproduction: False azalea resprouts from root crowns and adventitious stem buds after destruction of above-ground stems (Miller 1977; Coates 1987). The species also appears to be capable of layering by forming roots from adventitious buds along stems (C. Caza, pers. obs., 1987). Layering is an effective means of growth and expansion at high elevations where heavy snow loads press branches close to the ground.

EFFECTS ON CROP TREES

Competition: False azalea is a member of an ericaceous shrub complex common on NSR sites in the MH and ESSF in British Columbia. Other members of the complex include *Rhododendron albiflorum* and several *Vaccinium* species. Little is known about the effects of this complex on tree regeneration, but recent research by Coates (1987) suggested that impacts on light and soil temperatures may be involved in reduced tree seedling performance. Haeussler *et al.* (1984, 1985) did not consider false azalea to be a major brush species of the ICHg or CWHf, despite its presence in associations judged to be potential brush hazards in those subzones. Lloyd (1984) classified associations with the ericaceous shrub complex in the ESSFm and ESSFw of the North Thompson-Shuswap drainage as high brush hazards. Lowdermilk (1925) found both *Picea engelmannii* and *Abies lasiocarpa* regeneration coming up through dense stands of *M. ferruginea, Vaccinium* spp., *Pachystima myrsinites,* and *Rubus parviflorus* in the Colorado Rockies. He concluded that the reproduction of spruce was sufficient to replace natural mortality but not to restock a stand after harvesting.

There have been no reports of dense, pure populations of false azalea. It appears to occur typically as a greater or lesser component of different shrub complexes (Lowdermilk 1925; Brooke *et al.* 1970; Stickney 1980; Caza and Kimmins 1987). Consequently, studies of this species-competitive impact on tree seedlings should also consider its relative importance in comparison to associated vegetation. False azalea rarely appears to be the most aggressive member of a shrub complex (Miller 1977; Stickney 1980; Coates 1987).

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: In the cedar-hemlock forests of northern Idaho, there was no significant difference between the cover and frequency of false azalea on logged and unlogged sites (Mueggler 1965). Biomass of false azalea in early successional stands (up to 30 years) in southeastern Alaska was 3 times greater than the biomass in climax western hemlock - Sitka spruce forest (Alaback 1982).

Season of Logging: There appears to be little destruction of mature false azalea plants in spruce-fir forests when selective logging is done during the winter (Caza and Kimmins 1987; Coates 1987). If false azalea is a major component of the mature forest understory, it will continue to dominate the post-harvesting plant community. However, logging of ESSF forests with false azalea understories in the absence of snow cover appears to result in replacement of the shrub by such perennial herbs as *Valeriana sitchensis* and *Epilobium angustifolium.*

Fire: False azalea is a fire-sensitive species (Stickney 1981). Miller (1977) speculated that it would sprout from the root crown after a burn, but would not produce suckers. Fire appears to have totally

removed this species from experimental plots in Washington and Oregon, for up to 16 years (Morris 1970). In western Montana, Stickney (1981) found that survival of false azalea was low and it was very slow to redevelop after fire, especially on areas that had been intensely burned. However, Mueggler (1965) reported no significant difference in cover and frequency between burned and unburned areas in northern Idaho.

Herbicides: When glyphosate was applied to false azalea by Micron Herbi as a foliar spray at 500 g a.i./ha in the Kamloops Forest Region, many stems were at least partially killed, and 2 years later the foliage of surviving stems remained dwarfed and deformed.

Mechanical Site Preparation: Coates (1987) found that regrowth of false azalea in the ESSF after clipping and mechanical scarification was very limited, and confined to the production of new shoots from buds on old stems, rather than from basal sprouts or suckers. Two seasons after cutting, new shoots had not reached the height of precut stems, and did not overtop spruce or pine seedlings planted at the time of cutting.

Rhododendron albiflorum Hook. White-flowered rhododendron

(white rhododendron, mountain misery)

DESCRIPTION

White-flowered rhododendron is an erect, slender-branched shrub 1-2 m high with shedding bark. The deciduous leaves are up to 8 cm long and elliptic to oblong in shape. They are green above, paler below, and covered in loose reddish hairs, as are young twigs. Flowers are whitish or pale yellow, up to 2 cm long, and are borne along branches in clusters of 1-4 in the axil of the previous year's leaves. The fruit is an ovate capsule 6-8 mm long (Szczawinski 1962).

Variation: *Rhododendron* is a large genus with over 850 species throughout the world (Bowers 1960a). Many of these have been cultivated, and there are hundreds of horticultural varieties. *Rhododendron albiflorum* has not been cultivated successfully and because it is very difficult to grow outside its native habitat, it is considered to have little horticultural value. The species is morphologically distinct from all other rhododendrons and has been placed in its own series, Albiflorum. Taxonomically, it is most closely related to Asian species in the series Ovatum, and to the deciduous members of the large series Azalea, many of which have been intensively cultivated. No hybrids, subspecies, or varieties of *R. albiflorum* have been identified in British Columbia (Bowers 1960b; Szczawinski 1962).

DISTRIBUTION AND ABUNDANCE

White-flowered rhododendron is a species of mountainous areas. It is the only rhododendron found in the Rocky Mountains, and it is found throughout British Columbia up to 57°N latitude, although its occurrence north of 52°N is sparse. It has not been recorded south of Colorado. Although primarily a species of high elevations, white-flowered rhododendron is found as low as 250 m on the west coast of Vancouver Island. It typically occurs above 750 m in the Coast Range, and above 1200 m on the east side of the Fraser River and in the North Thompson-Shuswap drainage in the interior of British Columbia (Lloyd 1984).

White flowered rhododendron forms dense thickets above and below timberline. Because of its small leaf size, however, it does not form dense canopies.

Vegetation Associations: Within the province, white-flowered rhododendron is most abundant in the MH and ESSF, but it is also found in the AT, the upper CWH and ICH, and occasionally in the SBS. In the MH, white-flowered rhododendron is a characteristic understory species of *Tsuga mertensiana-Abies amabilis* forests, and often occurs with other ericaceous shrubs (Peterson 1965; Brooke *et al.* 1970). The *Vaccinium membranaceum-Rhododendron albiflorum* ecosystem association of the MH zone has its optimal development on mesic sites at 1200 m. However, this association can also develop at tree limit within this zone where it is found on drier, exposed ridges and forms a topographic climax. White-flowered rhododendron occurs throughout the ESSF in British Columbia. It is a characteristic species of the ESSFe zonal ecosystem association, where it is associated with *Vaccinium membranaceum, Valeriana sitchensis,* and *Orthilia secunda* (Mitchell and Green 1981). It is a differentiating species in the most productive association of the ESSFf for *Picea engelmannii* in southwestern British Columbia (Klinka *et al.* 1982). Within this association it is found with *Valeriana sitchensis* and *Ribes lacustre.* White-flowered rhododendron is found in many ecosystem associations of the ESSF subzones, in all nutrient regimes, and on all but the driest sites. It is a common understory component of the open subalpine forest, often associated with other ericaceous shrubs such as *Menziesia ferruginea* and *Vaccinium* spp. (Caza and Kimmins 1987). It occurs in more open subalpine environments in association with herbaceous species.

COMMENT

Very little is known about this species in comparison with other rhododendrons, primarily because of its lack of horticultural value. However, available information suggests that white-flowered rhododendron

shares some important ecological characteristics with other rhododendron species, both wild and cultivated, about which more is known.

HABITAT

Climatic Relations: Generally, rhododendrons are found only in areas with abundant moisture, and do not occur in arid regions of the world (Bowers 1960a). Members of the genus are not drought-tolerant and can only survive in cold climates where there is adequate protection from the drying effects of low temperatures and wind. White-flowered rhododendron grows in subalpine environments characterized by short growing seasons, high annual precipitation, and abundant snow. Evidence from other species suggests adequate snow cover may be a critical factor in protection from winter desiccation in white-flowered rhododendron (Bowers 1960b). Brooke *et al.* (1970) noted that, although the species grew in the MH zone in areas with maritime and continental climates, it was much more abundant in the latter. Its southern distribution may be limited by summer drought; its northern and altitudinal range may be limited by a combination of low temperature and winter snow cover.

Site and Soil Conditions: White-flowered rhododendron can be found growing on a wide range of site types, in mature, open forests, on cutovers after logging, and in subalpine meadows (Mitchell and Green 1981; Lloyd 1984; Caza and Kimmins 1987). In the open subalpine forests of the western North Cascades, the tree islands characteristic of these forests produced a very favourable microenvironment for the development of tall shrubs such as white-flowered rhododendron (Douglas 1972). Rhododendron populations found after logging in British Columbia are usually not newly established, but are residuals from the the preharvest forest, which have escaped destruction during harvesting. Rhododendrons, as a group, are surface-rooting plants (Bowers 1960a). Within British Columbia, parent materials on sites with white-flowered rhododendron are often colluvial or morainal deposits, and soils may be shallow. Soils with white-flowered rhododendron are typically humo-ferric podzols, occasionally dystric brunisols, and commonly have a Mor or Mormoder humus form (Mitchell and Green 1981; Klinka *et al.* 1982). Shaw (1984) showed that *Rhododendron ponticum* in Britain was associated with sites of high humidity and rainfall, northern aspects, steep slopes, and coarse rocky soils that did not dry out in summer. Evidence suggests that white-flowered rhododendron may have similar site preferences in British Columbia (Lloyd 1984; Caza and Kimmins 1987; Coates 1987).

Nutrient Relations: Members of the genus *Rhododendron* prefer or require acidic soils of pH 3.0-4.0 (Bowers 1960a; McGee and Smith 1967; Shaw 1984). Shaw (1984) noted that although adult plants of *R. ponticum* could survive at pH >5.0, their nutritional status was poor, and seedlings were killed at the higher pH. In British Columbia, white-flowered rhododendron has been reported as a significant species on soils with pH 4.0-5.5 (Brooke *et al.*1970; Mitchell and Green 1981; Lloyd 1984). There is no information available on the nutritional relations of white-flowered rhododendron. Nielsen and Wakefield (1978) concluded that competition for nitrogen and not phosphorus or potassium reduced growth and flowering by *Rhododendron* sp. in the presence of turfgrasses. However, they concluded that additions of fertilizer benefited grasses more than the shrubs, as the latter did not respond with increased growth. Yarie (1978) found that a shrub understory dominated by white-flowered rhododendron on xeric sites in the coastal Mountain Hemlock zone of British Columbia, played an important role in forest nutrient cycling. Understory vegetation returned a significant proportion of litterfall nutrients to the ecosystem each year, mainly in a single pulse during the first autumn snowfall. Understory vegetation also had a significant effect on the quantity of nutrients present in throughfall precipitation reaching the ground (Yarie 1978).

Water Relations: Rhododendrons do not occur in arid regions of the world, and members of the genus are generally only found in environments with abundant soil or atmospheric moisture (Bowers 1960a). In British Columbia, white-flowered rhododendron is found only in biogeoclimatic zones and subzones with high annual precipitation. However, within these areas it can be found on sites ranging from xeric to subhygric, though its best development is on mesic sites (Lloyd 1984; Caza and Kimmins 1987; Coates 1987). Leaves of other species of rhododendron have been shown to curl and droop in response to water stress, and these changes in leaf orientation can be permanent if growth occurs during a period of even temporary water stress (Nilsen 1986a).

Light Relations: In North America, optimal development of rhododendrons is associated with conditions of partial shade (Bowers 1960a). In the open, mature forests of the subalpine, white-flowered rhododendron is also most frequently associated with conditions of semishade (Peterson 1965; Douglas 1972). The response to different light regimes has been studied in several other species of rhododendron. Nilsen (1986a, 1986b) studied the phenological and physiological responses of *R. maximum* to light. He concluded that rhododendron leaves were very sensitive to light levels, and the rapid curling and angle changes displayed by *R. maximum* leaves prevented photo-oxidation (bleaching of chlorophyll) by high irradiance during cold weather, and thus reduced leaf mortality in this species. White-flowered rhododendron also appears to exhibit leaf curling but the ecological significance of the behaviour in this deciduous rhododendron is unknown.

Davis and Potter (1987) looked at the physiological response of *R. catawbiense* cuttings to 0, 50 and 95% shade treatments. They found that, despite initially greater photosynthetic rates, greater sucrose and starch levels, and lower water potentials under greater light levels, there were no differences in rooting percentage among the light treatments. After 23 weeks, plants under 95% shade were smaller, but the authors concluded that their vigour was unaffected as there were no differences in size among plants from the three treatments 2 months after outplanting.

Temperature Relations: Horticulturalists classify *Rhododendron albiflorum* as a hardy species, tolerant of low temperatures (Bowers 1960b). According to M. Burke (OSU Agricultural Sciences, pers. comm., 1988), white-flowered rhododendron is killed above ground at temperatures below -40°C, as a result of destruction of conducting tissues. Sakai *et al.* (1986) studied cold hardiness in 101 genotypes of *Rhododendron*. Flower buds and living xylem cells in rhododendrons survive freezing stress by deep supercooling, thereby avoiding ice crystallization in these tissues. If freezing occurs, these tissues die. Vegetative buds, evergreen leaves, and cortical tissues, on the other hand, only supercool a few degrees and survive freezing by tolerating ice formation within these tissues. Rhododendrons exhibit intraspecific differences in freezing resistance among climatic races. Iwaya-Inoue and Kaku (1983) looked at 24 species of rhododendrons (mostly azaleas), and found that within individual plants, tissues differed in their cold hardiness. Resistance increased from flower buds to bark and wood, to the most hardy tissue — the leaf bud. Nilsen (1985) found that leaf curling in *R. maximum* was highly associated with leaf temperature, with 0°C being the critical value stimulating the phenomenon of curling. Similarly, leaf angle was found to be linearly related to leaf temperatures above 0°C.

GROWTH AND DEVELOPMENT

Leaves of white-flowered rhododendron expand rapidly in the spring at high elevations in British Columbia. According to Brooke *et al.* (1970), the species has photosynthetic rates (APS) 3-5x greater than associated evergreen species after full leaf expansion. Longevity of individuals of white-flowered rhododendron is not known, but plants of other species in the genus may live over 100 years (Plocher and Carvell 1987). Evidence from other studies suggests that the growth and development of individuals of white-flowered rhododendron may vary significantly among environments (e.g., Mazurenko 1979). Nilsen (1986b) showed large differences in shoot growth, wood biomass, leaf survivorship, time of expansion, and water potentials of *R. maximum* plants grown under deciduous and evergreen canopies. He concluded that the major influence of canopy composition on growth and development in *R. maximum* was on relative dry weight allocation within plants. In higher irradiance environments (such as the deciduous forest), allocation favoured shoot and wood biomass, whereas in the lower irradiance conifer forest, allocation favoured leaf production. Nilsen cited results from several studies with other species of wild rhododendrons which have also shown reduced leaf area and survivorship in response to increased light levels associated with clearcutting and natural open communities (Nilsen 1986b).

Phenology: Flower production in white-flowered rhododendron occurs after leaf expansion in June in the subalpine environment. Shoot expansion occurs rapidly at the beginning of the short growing season, and leaf senescence can begin as early as August at higher elevations in British Columbia.

REPRODUCTION

Seed Production and Dispersal: Seeds of the genus *Rhododendron* are among the smallest of the plant kingdom (Cross 1981). The USDA (1974) measured 4-13 million per kilogram. The capsule of white-flowered rhododendron dehisces, releasing seeds with winged margins, which are wind-dispersed (Szczawinski 1962). The success of the introduced species, *R. ponticum*, in Britain is largely attributed to the copious seed produced and the effectiveness of dispersal of the small seed into all environments (Cross 1981; Tabbush and Sale 1984).

Seed Viability and Germination: The viability of the seeds of some rhododendron species has been found to vary under natural conditions, but is not generally greater than 1 year (Cross 1981), unless conditions are very dry. Germination requirements in species such as *R. ponticum* are rigorous, with light, humidity and protection from physical elements necessary for the survival of the fragile and slow-growing seedling (Cross 1981). Cross (1981) reported that *R. ponticum* seedlings were vulnerable to drought, and that the distribution of seedlings in forests was not random, but strongly associated with low-growing mosses. Very few seedlings were found under herbaceous cover or on bare soil. Plocher and Carvell (1987) also found that seedling establishment in *R. maximum* was associated with moss-covered substrates.

Studies on both *R. ponticum* and *R. maximum* have shown there is little regeneration by seed in established thickets of these species (McGee and Smith 1967; Tabbush and Sale 1984). Once established, there is very little recruitment within thickets of undisturbed rhododendron, and very little expansion in total area (McGee and Smith 1967; Plocher and Carvell 1987). Seedlings cannot establish within mature thickets, and sprouts that are produced within this environment are usually short-lived.

Vegetative Reproduction: White-flowered rhododendron shares a similar growth habit with *R. maximum*, which forms dense thickets in forests of higher elevations in the Appalachians. Both are capable of resprouting from the root crown and adventitious stem buds, as well as of layering (formation of adventitious roots from dormant buds on shoots). These forms of vegetative growth are widespread among rhododendrons. Mazurenko (1979) observed growth of dormant buds 10-20 years old on shoots of *R. aureum* in the USSR. Layering is a very useful strategy for expansion in subalpine environments where snow loads and snow creep on slopes keep lower branches pressed close to the ground. Any expansion that occurs in established thickets of these species is by layering, and Plocher and Carvell (1987) found this process to be favoured by wetter conditions, denser thickets, and well-developed herbaceous vegetation.

PREDATION AND PESTS

In general, Rhododendrons are unpalatable to livestock and wild grazing animals (Nilsen 1986b). Shaw (1984) claimed that unpalatability of *R. ponticum* and its freedom from pests and diseases were major factors in the success of this species as a forest weed in Britain. It is not grazed because plants contain the compound andromedotoxin, which is highly toxic to animals (Cross 1981).

INTERACTIONS WITH CROP TREES

Competition: White-flowered rhododendron is one of the species of an ericaceous shrub complex that is common on NSR sites in the ESSF and MH zones of southern British Columbia. The other major species of this complex are *Menziesia ferruginea* and several *Vaccinium* spp. (Caza and Kimmins 1987; Coates 1987). The complex is often associated with poor post-logging regeneration of conifers. The complex may influence tree regeneration by affecting soil temperature, chemistry (pH and allelopathy), light, snow and frost characteristics, and soil moisture; or it may have direct mechanical effects on tree seedlings. The magnitude and relative importance of these factors is not well understood, but Coates (1987) suggests that effects of the shrub on both light and soil temperature may be important in reduced performance of planted conifer seedlings. Del Moral and Cates (1971) showed that both leaves and litter of white-flowered rhododendron produced volatile and water-soluble chemicals capable of inhibiting laboratory germination of *Hordeum* seeds. They noted also that fewer species occurred beneath the canopy of white-flowered rhododendron in the field than were present adjacent to the shrub, and concluded that the shrub may be allelopathic to

other plants. Cross (1981) and Miles (1985) both noted that *R. ponticum* was a successful competitor in Britain because of its ability to shade out other vegetation.

Similarly, white-flowered rhododendron has an open habit and does not produce a deep canopy, but its longevity, shade tolerance, and apparent freedom from predators may provide it with a strong competitive ability. Phillips and Murdy (1985) found that *R. maximum* had a negative impact on hardwood regeneration, with sapling recruitment into the overstory canopy decreasing with increasing rhododendron density. However, the number of seedlings of the only conifer present, a hemlock species, increased with increasing density of the shrub. The authors also noted that the major cause of *R. maximum* seedling mortality appeared to be competition with established *R. maximum* plants. Despite Phillips and Murdy's findings, Plocher and Carvell (1987) noted that both hardwood and conifer regeneration were common in dense *R. maximum* thickets, indicating that tree seedling establishment is possible within the rhododendron environment.

Beneficial Effects: On dry or exposed sites, white-flowered rhododendron may provide some shade and reduce evapotranspiration in young seedlings. Several high-elevation coniferous species have also been shown to be vulnerable to photo-oxidation at high light intensities (Ronco 1970). Partial shade may be beneficial under these conditions to prevent chlorophyll bleaching and damage to the photosynthetic mechanism.

RESPONSE TO DISTURBANCE OR MANAGEMENT

Research is now under way in British Columbia on the response of white-flowered rhododendron to vegetation management treatments (D. Coates, Skeena Forestry Consultants, Smithers, B.C., pers. comm., 1987; C. Caza, pers. comm., 1988; D. Lloyd, Ministry of Forests, Kamloops, B.C., pers. comm., 1988). However, there has been considerable research by horticulturalists on the effects of herbicides on ornamental rhododendrons, as well as research by ecologists and foresters on management of *R. ponticum* and *R. maximum*, major forest weeds of Britain and eastern North America, respectively. Herbicides that have been found to severely damage but not kill ornamental rhododendrons and azaleas include bentazon and oxyfluorofen (Kuhns and Haramaki 1980); asulam, glyphosate, pronamide, and methazole (Frank and Beste 1986); and oxadiazon (Glaze *et al.* 1987). However, azalea plants with shoots killed by asulam have been shown to recover their growth quickly (Ahrens 1974). The amount of damage caused by these herbicides varied with method, rate, and time of application, and, to some extent, with species. Shaw (1984) noted that attempts to control *R. ponticum* in Britain through mechanical removal of older bushes have been largely unsuccessful because of regrowth from buried fragments and creation of good conditions for re-establishment. Tabbush and Sale (1984) tested several herbicides for efficacy against *R. ponticum*. Glyphosate and triclopyr were effective in killing plants, but hexazinone was not. Triclopyr at 4 kg a.e./ha, was more effective than glyphosate at 4 kg a.i./ha. Glyphosate was less effective at controlling this species when applied at 2 kg a.i./ha than at 4 kg a.i./ha. The authors recommend a volume rate of 40-60 L/ha using 9 L/ha of glyphosate for *R. ponticum*. The authors concluded that control should be aimed at regrowth and small bushes, as control of mature plants was expensive and impractical. Neary *et al.* (1979, 1984), using picloram pellets to kill *R. maximum* observed between 32 and 36% mortality of stems and over 95% damage to rhododendron with broadcast applications in spring.

Coates (1987) found that regrowth of white-flowered rhododendron after clipping and mechanical scarification was very limited and involved the production of new shoots from buds on old stems rather than basal sprouts or suckers. Two seasons after cutting, new shoots had not reached the height of precut stems, and did not overtop spruce or pine seedlings planted at the time of cutting.

Rubus parviflorus Nutt. — Thimbleberry

DESCRIPTION

Thimbleberry is an erect shrub which grows to 2.5 m tall. Stems are unarmed and have gray flaking bark. Leaves are deciduous, palmately lobed, and usually large (up to 25 cm long). Showy white flowers develop during spring and summer in terminal inflorescences. Soft, dull, red thimbleberry fruit develops during the summer; the berries are composed of many small hairy drupelets (Moss 1959; Hitchcock *et al.* 1961; Viereck and Little 1972; Garman 1973; Taylor 1973; Clark 1976; Patterson *et al.* 1985).

DISTRIBUTION AND ABUNDANCE

Thimbleberry is widespread in North America. Its range extends from Alaska south to Northern Mexico and from the west coast east to Ontario and Minnesota (Hitchcock *et al.* 1961; Viereck and Little 1972; Scoggan 1978). It is common north to 56°N latitude in the British Columbia Interior, and along the entire length of the coast including Vancouver Island and the Queen Charlotte Islands. Thimbleberry is present in most biogeoclimatic zones of British Columbia, with the exception of the SWB and parts of the BWBS outside of the Peace River valley. Thimbleberry is most common in moist or wet subzones of the coast and Interior, and is very rare in the PP, BG, and dry subzones of the IDF (Angove and Bancroft 1983). Douglas (1972) reports that thimbleberry is common at elevations of 1800 m in the western north Cascades of Washington.

Thimbleberry abundance may range from sparse scattered individuals up to 100% canopy cover. Its abundance appears to be related to time since disturbance, tree canopy cover, and site factors.

HABITAT

Climatic Relations: Thimbleberry tolerates a wide range of climatic conditions in British Columbia, with the exception of the boreal region where winters are extremely cold and the growing season is short. It is more abundant in cool moist areas which may explain its reported preference for north aspects in areas such as northern Idaho (Irwin and Peek 1979). This species does not tolerate the extreme summer droughts that are encountered in the PP and BG zones, and dry subzones of the IDF in the southern Interior.

Site and Soil Conditions: Thimbleberry can be found growing on a wide variety of soils and landforms in open areas as well as under the canopy of forest stands. It can be found growing in open forests, on roadsides, in cutover lands, meadows, and avalanche tracks, and in riparian habitats (Viereck and Little 1972; Taylor 1973; Gratkowski 1978). In northern Idaho, it is most common in *Abies grandis*, *Thuja plicata*, and *Tsuga heterophylla* habitat types (Patterson *et al.* 1985). In British Columbia, it is common as an understory species on sites in the CWH, SBS, ICH, MS, and ESSF zones on a variety of soils developed from a diversity of parent materials.

Nutrient Relations: Thimbleberry grows under a wide range of nutrient conditions. Most vigourous growth of thimbleberry is usually found on base-rich sites. Wali (1969) reports that this species is found in the SBS on sites with a wide range of available calcium. Pojar *et al.* 1982 report that thimbleberry grows on all but very nutrient poor soils in the SBS.

Water Relations: Thimbleberry occurs on sites with moisture regimes ranging from submesic to hygric (Pojar *et al.* 1982; Angove and Bancroft 1983). It is most vigourous and most abundant on subhygric and hygric sites with well-aerated soils. It will reproduce and grow on relatively drier sites, but it usually achieves low cover and small stature (Clark 1976; Marchant and Sherlock 1984).

Light Relations: Thimbleberry grows under closed canopies of coniferous or deciduous forest stands and in open meadows and clearings. Cover and vigour of thimbleberry is usually greatest under partially open or open conditions. As tree basal area and canopy cover increase and understory light intensity declines, thimbleberry cover and vigour also decline (Mueggler 1965; Irwin and Peek 1979). Emmingham (1972) reports that thimbleberry may grow under forest canopies where plants receive as little as 3.5% of full sunlight.

GROWTH AND DEVELOPMENT

No published studies dealing specifically with the growth and development of thimbleberry are available. It is a rhizomatous species with perennial canes (Viereck and Little 1972). Canes usually live for 2 or 3 years, and produce flowers and fruit on short lateral branches during the 2nd year.

Under favourable conditions, thimbleberry plants can grow rapidly. Dense cover can be achieved in as little as 5 or 6 years (Eis 1981; Morgan 1984) following disturbance. Stickney (1985) reports that thimbleberry achieved maximum cover within 4 years on the Sundance Burn in northern Idaho. Thimbleberry can achieve leaf area indexes of 10 m^2/m^2 in communities growing on moist sites in the southern Interior (P. Comeau, unpubl. data) and a maximum height of 2-2.5 m within 15-25 years of release (Mueggler 1965; Laursen 1984). Thimbleberry growing from rhizomes on moist sites in the British Columbia Interior and coast can reach 2 m height in less than 10 years. Maximum rates of height growth have been observed during the 2nd and 3rd year.

Phenology: In western Oregon and Washington, vegetative buds of thimbleberry can become active as early as late February (Stewart 1974a). In northern Idaho and western Montana, bud burst takes place between early April and early June depending on elevation and weather conditions. Leaves are fully grown approximately 1 month after bud burst. Leaf senescence typically begins by late August and leaf fall extends from late August to mid- to late October in Idaho and Montana (Schmidt and Lotan 1980). Data from the central coast of British Columbia indicate similar timing of vegetative events.

Flowering can extend from early May to early August, but is centred on the months of June and July in Alaska (Viereck and Little 1972), Idaho, and Montana (Schmidt and Lotan 1980). In British Columbia, fruits ripen from early June to mid-September, depending on elevation and other local factors (Marchant and Sherlock 1984).

REPRODUCTION

Seed Production and Dispersal: The berry-like fruit of thimbleberry contains many small seeds. Seed production can be sparse at high elevations. Once ripe, the fruit falls readily to the ground (Marchant and Sherlock 1984). Wider dispersal of the seed is primarily by birds (Core 1974; M. Newton, pers. comm., Dec. 1984), but also by mammals feeding on the fruit.

Seed Viability and Germination: Seeds of thimbleberry are believed to remain viable for a long period of time, like those of other members of the *Rubus* genus. Kellman (1970) found buried viable seeds of thimbleberry (18 seeds per square metre) in a soil core taken from a mature conifer forest near Haney, B.C. Morgan (1984) found as many as 84 seeds per square metre in forest soils in Idaho.

Thimbleberry seeds present in soil seedbanks are viable (Olmsted and Curtis 1947). Mild heat scarification appears to improve their germination in forest soils (Morgan 1984). Allelopathic effects of bracken and other species may inhibit germination of thimbleberry seeds (Stewart 1975). The seed has moderate viability in germination tests (maximum 62%), and requires approximately 90 days of chilling to germinate. Acid treatment may also promote germination (Marchant and Sherlock 1984). Germination of buried and newly deposited seed is believed to be the principal means by which thimbleberry invades new areas. Abundant seedlings are present on disturbed sites within the 1st year following disturbance (Kelpsas 1978; Stewart 1978).

Vegetative Reproduction: Thimbleberry is a strongly rhizomatous species (Stickney 1981; Crane *et al.* 1983; Marchant and Sherlock 1984; Morgan 1984), and once it is established on a site, further expansion of the colony is achieved through the spread of rhizomes. The species can be readily propagated from cuttings and fragments of rhizomes (Hungerford 1984; Marchant and Sherlock 1984).

PREDATION AND PESTS

Thimbleberry fruit and leaves are eaten by many birds and mammals (Olmsted and Curtis 1947). Voth *et al.* (1983) report that, in Oregon, thimbleberry leaves represented approximately 3% of the annual diet and 14% of the November diet of white-footed voles.

Thimbleberry fruit sustains less damage from raspberry beetle than *Rubus idaeus* cultivars (Briggs *et al.* 1982). Thimbleberry is also resistant to raspberry cane midge (McNicol *et al.* 1983). Some species of aphid (*Masonaphis* spp.) occur widely on thimbleberry (Frazer and Forbes 1968; Gilbert and Gutierrez 1973; Gilbert 1980a, 1980b), but their impact on plant growth is not known. Conspicuous galls occur on thimbleberry over much of western North America. These are caused by the cyanid wasp (*Diastrophus kincaidii*) (Wangberg 1975).

EFFECTS ON CROP TREES

Competition: On some moist, cool sites, thimbleberry can establish dense canopies. Under these canopies less than 1% of full sunlight may reach overtopped seedlings (P. Comeau, unpubl. data). However, since thimbleberry leaves and canopies are often not fully developed until late July, the impact of thimbleberry cover on seedling growth may be substantially less than that of evergreen shrubs or early season deciduous shrubs and herbs. Evidence from a study conducted near Chilliwack (J.P. Kimmins and J. Karakatsoulis, unpubl. data) suggests that thimbleberry may also compete with tree seedlings for water during dry summer periods.

Extracts of thimbleberry foliage and litter inhibited seed germination and radical elongation (of two grasses and Douglas-fir) under laboratory conditions (Del Moral and Cates 1971). However, no evidence of allelopathic effects of thimbleberry were observed under field conditions.

The presence of other vegetation interferes with the establishment of thimbleberry (Eis 1981). Stickney (1981) reports that thimbleberry establishes and grows slowly when fireweed has colonized a site. In the SBS zone near Prince George, thimbleberry cover 6 years after clearcutting was greater on a Devil's Club site (40%) than on an alluvium site (15%) where it faced greater competition from other shrub species (Eis 1981). Allelopathic effects of plants such as western bracken (Stewart 1975) may reduce germination and growth of thimbleberry.

Beneficial Effects: Light to moderate thimbleberry cover may provide shade for establishing seedlings and reduce physiological stresses. The degree to which such vegetation cover is beneficial to seedling establishment and growth depends on environmental conditions, vegetation cover, and the duration of the vegetation canopy.

RESPONSE TO DISTURBANCE AND MANAGEMENT

Forest Canopy Removal: Thimbleberry may grow rapidly following removal of overtopping canopies (Wittinger *et al.* 1977; Irwin and Peek 1979). When disturbed, its primary mode of regeneration is by resprouting from existing rhizomes. However, thimbleberry may also establish from seed (Morgan 1984). It may achieve heights of 2-2.5 m within 10 years of release (Mueggler 1965; Laursen 1984; Miller 1986a).

Maximum cover may be achieved within 8 to 25 years following disturbance (Laursen 1984; Stickney 1985). Cover of thimbleberry declines as tree canopy cover and basal area increases (Mueggler 1965; Irwin and Peek 1979; Laursen 1984).

Fire: Rhizomes of thimbleberry can survive fire and resprout vigourously (Wright 1972; Crane *et al.* 1983), and thimbleberry can seed in on unoccupied ground (Stewart 1978; Morgan 1984). Thimbleberry may achieve maximum cover within 3-5 years following fire (Lafferty 1972; Dyrness 1973; Crane *et al.* 1983; Cholewa and Johnson 1983; Morgan 1984; Stickney 1985). Cover of thimbleberry is often greater on burned sites than on unburned sites (Lafferty 1972; Wittinger *et al.* 1977). Low intensity burns often lead to most rapid development of thimbleberry cover (Lafferty 1972; Morgan 1984). Early dominance of sites by more aggressive species such as fireweed can delay development of thimbleberry cover (Stickney 1981). If fire selectively eliminates other species, thimbleberry may replace them (Junke *et al.* 1978; Stickney 1981).

Manual Treatments: Manual cutting generally gives ineffective control of thimbleberry (Expert Committee on Weeds 1987). Thimbleberry resprouts rapidly following cutting and often returns to its original height and cover within 1 year of cutting (Coates and Haeussler 1986).

Herbicides: Foliar application of glyphosate during summer or fall is effective for controlling thimbleberry (Conard and Emmingham 1983, 1984; Expert Committee on Weeds 1985, 1986, 1987; Coates and Haeussler 1986; Miller 1986b; William *et al.* 1987). Spring foliar application of 2,4-D gave effective control of thimbleberry in northeastern Oregon and northern Idaho (Conard and Emmingham 1983; Hann 1986). In coastal areas, 2,4-D has given variable results (Conard and Emmingham 1984). Application of triclopyr as a foliar spray in spring, late summer, or fall gives moderate control of thimbleberry (Warren 1982; Conard and Emmingham 1983, 1984; Expert Committee on Weeds 1986; William *et al.* 1987). Basal and late dormant applications of triclopyr may also give control of thimbleberry (Warren 1982; Hamel 1983).

Thimbleberry appears to be resistant to hexazinone (Expert Committee on Weeds 1984, 1986). Sulfometuron methyl (Oust®) applied at either 150 or 600 g a.i./ha gives effective control of thimbleberry (Expert Committee on Weeds 1986). Tests of other herbicides are described by Stewart (1974a, 1974b, 1974c), Gratkowski (1978), and Hamel (1983).

Soil Disturbance: Thimbleberry may re-establish rapidly following soil disturbance (Dyrness 1973; Arno *et al.* 1985). It quickly invades disturbed soils by resprouting from rhizomes or through germination of seeds. On moist, rich sites it may redevelop rapidly from rhizomes and produce dense cover as much as 1 m tall within 3 years of disturbance (Arlidge 1967).

LITERATURE CITED

Ahlgren, C.E. 1960. Some effects of fire on reproduction and growth of vegetation in northeastern Minnesota. Ecology 41:431-445.

Ahlgren, C.E. and I.F. Ahlgren. 1981. Some effects of different forest litters on seed germination and growth. Can. J. For. Res. 11:710-714.

Ahrens, J.F. 1974. Selectivity of glyphosate and asulam in ornamental plantings and Christmas trees. Proc. NE. Weed Control Conf. 28:361-367.

Alaback, P.B. 1982. Forest community structural changes during secondary succession in southeast Alaska. *In* Forest succession and stand development research in the northwest. Symp. Proc.. Oreg. State Univ., Corvallis, Oreg., pp. 770-779.

Angove, K. 1981. A guide to some common plants of the Kamloops region, British Columbia. B.C. Min. For., Land Manage. Handb. No. 3.

Angove, K. and B. Bancroft. 1983. A guide to some common plants of the southern interior of British Columbia. B.C. Min. For., Land Manage. Handb. No. 7.

Archibold, O.W. 1980. Seed input into a postfire forest site in northern Saskatchewan. Can. J. For. Res. 10:129-134.

Arlidge, J.W.C. 1967. The durability of scarified seedbeds for spruce regeneration. B C. For. Serv. Res. Notes No. 42.

Arno, S.F., D.G. Simmerman, and R.F. Keene. 1985. Forest succession on four habitat types in western Montana. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. INT-177.

Bailey, J.A. and D. Hoogland. 1984. The response of *Epilobium* species to a range of soil and foliar-acting herbicides. Aspects Appl. Biol. 8:43-52.

Bartos, D.L. and W.F. Mueggler. 1981. Early succession in aspen communities following fire in western Wyoming. J. Range Manage. 34(4):315-318.

Behrend, D.F. and E.F. Patric. 1969. Influence of site disturbance and removal of shade on regeneration of deer browse. J. Wildl. Manage. 33:394-398.

Benecke, J. 1970. Nitrogen fixation by *Alnus viridis* (Chaix) DC. Plant and Soil 33:30-48.

Bevington, J. 1986. Geographic differences in the seed germination of paper birch (*Betula papyrifera*). Amer. J. Bot. 73(4):564-573.

Binkley, D. 1982. Nitrogen fixation and net primary production in a young Sitka alder stand. Can. J. Bot. 60:281-284.

_____. 1984. Douglas-fir stem growth per unit of leaf area increased by interplanted Sitka alder and red alder. For. Sci. 30:259-263.

Binkley, D., J.D. Lousier, and K. Cromack Jr. 1984. Ecosystem effects of Sitka alder in a Douglas-fir plantation. For. Sci. 30:26-35.

Bjorkbom, J.C. 1967. Seedbed preparation methods for paper birch. U.S. Dep. Agric. For. Serv., Res. Pap. NE-79.

_____. 1972. Ten-year growth of planted paper birch in old fields in Maine. U.S. Dep. Agric. For. Serv., Res. Pap. NE-246.

_____. 1973a. Response of paper birch seedlings to nitrogen, phosphorus, and potassium. U.S. Dep. Agric. For. Serv., Res. Note NE-157.

_____. 1973b. The effects of various combinations of nitrogen, phosphorus, and potassium on paper birch seedling growth. U.S. Dep. Agric. For. Serv., Res. Note NE-158.

Bjorkbom, J.C., D.A. Marquis, and F.E. Cunningham. 1965, The variablility of paper birch seed production, dispersal, and germination. U.S. Dep. Agric. For. Serv., Res. Pap. NE-41.

Blackmore, D.G. and G. Corns. 1979. Lodgepole pine and white spruce establishment after glyphosate and fertilizer treatments of grassy cutover forest land. For. Chron. 55:102-105.

Bollen, W.B., K.C. Lu, J.M. Trappe, and R.F. Tarrant. 1969. Influence of Sitka alder on soil formation and microbiological succession on a land slide of alpine origin at Mount Rainier. U.S. Dep. Agric. For. Serv., Pac. NW For. Range Exp. Stn., Res. Notes 103:1-5.

Bowers, C.G. 1960a. Rhododendrons in the wild. *In* Rhododendrons and azaleas. 2nd ed. Macmillan Company, New York, N.Y., pp. 16-25.

_____ . 1960B. Albiflorum series. *In* Rhododendrons and azaleas. 2nd ed. Macmillan Company, New York, N.Y., p. 231.

Boyd, R.J., D.L. Miller, F.A. Kidd, and C.P. Ritter. 1985. Herbicides for forest weed control in the inland northwest: a summary of effects on weeds and conifers. U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. INT-195.

Braekke, F.H. and T.T. Kozlowski. 1975. Effect of climatic and edaphic factors on radial stem growth of *Pinus resinosa* and *Betula papyrifera* in northern Wisconsin. Adv. Front. Pl. Sci. 30:201-221.

Brayshaw, T.C. 1978. Catkin bearing plants (Amentiferae) of British Columbia. Occasional papers of the B.C. Prov. Museum No. 18, Victoria, B.C., pp. 136, 144-145.

Briggs, J.B., J. Danek, M. Lyth, and E. Keep. 1982. Resistance to raspberry beetle, *Byturus tomentosus*, in *Rubus* species and their hybrid derivatives with *R. idaeus*. J. Hortic. Sci. 57:73-78.

Brittain, W.H. and W.F. Grant. 1966. Observations on Canadian birch (Betula) collections at the Morgan arboretum. III. *B. papyrifera* of British Columbia. Can. Field Nat. 80:147-157.

_____ . 1968. Observations on Canadian birch (Betula) collections at the Morgan arboretum. VI. *B. papyrifera* from the Rocky Mountains. Can. Field Nat. 82:44-48.

Brooke, R.C. 1965. The subalpine mountain hemlock zone. Part II. Ecotopes and biogeocoenotic units. Ecol. West. Nor. Am. 2:79-101.

Brooke, R.C., E.B. Peterson, and V.J. Krajina. 1970. The subalpine mountain hemlock zone. Ecol. West. Nor. Am. 2(2):147-349.

Bryant, J.P., F.S. Chapin, D.B. Reichardt, and T.P. Clausen. 1987. Response of winter chemical defense in Alaska paper birch and green alder to manipulation of plant carbon/nutrient balance. Oecol. 72:510-514.

Burns, R.M. (compiler). 1983. Silvicultural systems for the major forest types of the United States. U.S. Dep. Agric., For. Serv. Handb. No. 445.

Carpenter, C.V., L.E. Baribo, L.R. Robertson, F. Van DeBogart and G.M. Onufer. 1979. Acetylene reduction by excised root nodules from *Alnus rubra* and *Alnus sinuata*. *In* Symbiotic nitrogen fixation in the management of temperate forests. J.C. Gordon, C.T. Wheeler, and D.A. Perry (editors). Oreg. State Univ., Corvallis, Oreg. 475 p.

Carpenter, C.V. and L.R. Robertson. 1984. The effect of four new Frankia isolates on growth and nitrogenase activity in clones of *Alnus rubra* and *Alnus sinuata*. Can. J. For. Res. 14:701-706.

Caza, C.L. and J.P. Kimmins. 1987. Composition and structure of plant communities on NSR cutovers in the ESSF, Clearwater Forest District. FRDA Contract 3.32 Southern Interior. B.C. Min. For., Kamloops Region. Kamloops, B.C. 96 p.

Chapin, F.S., III, P.R. Tryon, and K. van Cleve. 1983. Influence of phosphorus on growth and biomass distribution of Alaskan taiga tree seedlings. Can. J. For. Res. 13:1092-1098.

Cholewa, A.F. and F.D. Johnson. 1983. Secondary succession in the *Pseudotsuga menziesii/ Physocarpus malvaceous* association. NW Sci. 57:273-282.

Clark, L.J. 1976. Wildflowers of the Pacific Northwest from Alaska to northern California. Gray's Publishing, Sidney, B.C.

Clark, M.B. and A. McLean. 1975. Growth of lodgepole pine seedlings in competition with different densities of grass. B.C. For. Serv., Res. Note No. 70. 10 p.

Cline, R.G. and G.S. Campbell. 1976. Seasonal and diurnal water relations of selected forest species. Ecology 57:367-373.

Coates, D. 1987. Effects of shrubs and herbs on conifer regeneration and microclimate in the Rhododendron-Vaccinium-Menziesia community of south-central British Columbia. M.Sc. thesis. Oreg. State Univ., Corvallis, Oreg. 93 p.

Coates, D. and S. Haeussler. 1986. A preliminary guide to the response of major species of competing vegetation to silvicultural treatments. B.C. Min. For., Land Manage. Rep. No. 9.

Conard, S.G. and W.H. Emmingham. 1983. Herbicides for shrub control on forest sites on northeastern Oregon and northern Idaho. Oreg. State Univ., For. Res. Lab., Special Bull. No. 5. 8 p.

_____ . 1984. Herbicides for brush and fern control on forest sites in western Oregon and Washington. Oreg. State Univ., For. Res. Lab., Special Publ. No. 8. 8 p.

Conklin, J.G. 1969. Insect enemies of birch. *In* Birch Symp. Proc.. U.S. Dep. Agric. For. Serv., NE For. Exp. Stn. pp. 151-154.

Conn, J.S. and J.A. DeLapp. 1983. Changes in weed-species assemblage with increasing field age. Agroborealis 15:39-41.

Core, E.L. 1974. Brambles. In Shrubs and vines for northeastern wildlife. J.D. Gill and W.M. Healy (editors). U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. NE-9, pp. 16-19.

Corns, I.G.W. and G.H. La Roi. 1976. A comparison of mature with recently clear-cut and scarified lodgepole pine forests in the Lower Foothills of Alberta. Can. J. For. Res. 6:20-32.

Crane, M.F., J.R. Habeck, and W.C. Fischer. 1983. Early postfire revegetation in a western Montana Douglas-fir forest. U.S. Dep. Agric. For. Serv., Res. Pap. INT-319. 32 p.

Crocker, R.L. and B.A. Dickson. 1957. Soil development on the recessional moraines of the Herbert and Mendenhall glaciers, south-eastern Alaska. J. Ecol. 45:169-185.

Crocker, R.L. and J. Major. 1955. Soil development in relation to vegetation and surface age at Glacier Bay, Alaska. J. Ecol. 43:427-448.

Cross, J.R. 1981. The establishment of *Rhododendron ponticum* in the Killarney Oakwoods. S.W. Ireland. J. Ecol. 69:807-824.

Dalton, D.A. and A.W. Naylor. 1975. Studies on nitrogen fixation by *Alnus crispa*. Amer. J. Bot. 62(1):76-80.

Davis, T.D. and J.R. Potter. 1987. Physiological response of Rhododendron cuttings to different light levels during rooting. J. Am. Soc. Hortic. Sci. 112(2):256-259.

Dawson, J.O. and J.C. Gordon. 1979. Nitrogen fixation in relation to photosynthesis in *Alnus glutinosa*. Bot. Gaz. 140(Suppl.):S70-S75.

Del Moral, R. and R.G. Cates. 1971. Allelopathic potential of the dominant vegetation of western Washington. Ecology 52:1030-1037.

Dimock, E.J. II, T.F. Beebe, and E.B. Collard. 1983. Planting-site preparation with herbicides to aid conifer reforestation. Weed Sci. 31:215-221.

Douglas, G.W. 1972. Subalpine plant communities of the western North Cascades, Washington. Arctic and Alpine Res. 4:147-166.

Dyrness, C.T. 1965. The effect of logging and slash burning on understory vegetation in the H.J. Andrews experimental forest. U.S. Dep. Agric. For. Serv., Res. Note PNW-31.

_____ . 1973. Early stages of plant succession following logging and burning in the western Cascades of Oregon. Ecology 54:57-69.

Dyrness, C.T. and R.A. Norum. 1983. The effects of experimental fires on black spruce forest floors in interior Alaska. Can. J. For. Res. 13:879-893.

Economou, A.S. and P.E. Read. 1986. Influence of pH and medium composition on rooting of hardy deciduous azalea microcuttings. J. Am. Soc. Hortic. Sci. 111(2):181-184.

Eis, S. 1981. Effect of vegetative competition on regeneration of white spruce. Can. J. For. Res. 11:1-8.

Elias, T. S. 1980. The alder genus. *In* The complete trees of North America. Van Nostrand Reinhold Co., New York, N.Y. pp. 403-406.

Emmingham, W.H. 1972. Conifer growth and plant distribution under different light environments in the Siskiyou mountains of southwestern Oregon. M.S. thesis. Oreg. State Univ., Corvallis, Oreg.

Ericsson, K.A. and D.F. Schimpf. 1986. Woody riparian vegetation of a Lake Superior tributary. Can. J. Bot. 64:769-773.

Etherington, J.R. 1983. Control of germination and seedling morphology by ethene: differential responses, related to habitat of *Epilobium hirsutum* L. and *Chamerion angustifolium* (L.) J. Holub. Ann. Bot. 52:633-658.

_____. 1984. Comparative studies of plant growth and distribution in relation to waterlogging. X. Differential formation of adventitious roots and their experimental excision in *Epilobium hirsutum* and *Chamerion angustifolium*. J. Ecol. 72:389-404.

Expert Committee on Weeds. 1984. Expert Committee on Weeds, Research Report. Western Canada Section Meeting, December 3-6, 1984. Winnipeg, Man.

_____. 1985. Expert Committee on Weeds, Research Report. Western Canada Section Meeting, December 3-5, 1985. Edmonton, Alta.

_____. 1986. Expert Committee on Weeds, Research Report. Western Canada Section Meeting, November 25-27, 1986. Saskatoon, Sask.

_____. 1987. Expert Committee on Weeds, Research Report. Western Canada Section Meeting, December 1-3, 1987. Victoria, B.C.

Filauro, A. 1982. TSI on northern hardwoods using triclopyr or hexazinone. Proc. NE Weed Sci. Soc. 36:229-233.

Fletcher, K. and V.C. Brink. 1969. Content of certain trace elements in range forages from south central British Columbia. Can. J. Plant Sci. 49:517-520.

Foote, M.J. 1983. Classification, description, and dynamics of plant communities after fire in the taiga of interior Alaska. U.S. Dep. Agric. For. Serv., Res. Pap. PNW-307. 108 p.

Ford, E.D. and E. Renshaw. 1984. The interpretation of process from pattern using two-dimensional spectral analysis: modelling single species patterns in vegetation. Vegetatio 56:113-123.

Foster, D.R. 1984. Phytosociological description of the forest vegetation of southeastern Labrador. Can. J. Bot. 62:899-906.

_____. 1986. Vegetation development following fire in *Picea mariana* (black spruce) - Pleurozium forests of southeastern Labrador, Canada. J. Ecol. 73:517-534.

Foster, D.R. and G.A. King. 1986. Vegetation pattern and diversity in S.E. Labrador, Canada: *Betula papyrifera* (birch) forest development in relation to fire history and physiography. J. Ecol. 74:465-483.

Fowells, H.A. (compiler). 1965. Silvics of forest trees of the United States. U.S. Dep. Agric. For. Serv., Handb. No. 271.

Frank, J.R. and C.E. Beste. 1986. Postemergence control of weeds in azaleas with sethoxydim and fluazifop. HortScience 21(6):1400-1403.

Frazer, B.D. and A.R. Forbes. 1968. *Masonaphis maxima* (Mason) (Homoptera: Aphididae), an aphid on thimbleberry with an unusual life history. J. Entomol. Soc. B.C. 65:36-39.

Fredskild, B. 1984. Distribution and occurrence of Onagraceae in Greenland. Nord. J. Bot. 4:475-480.

Freyman, S. 1970. Effects of clipping on pinegrass. Can. J. Plant Sci. 50:736-739.

Freyman, S. and A.L. van Ryswyk. 1969. Effect of fertilizer on pinegrass in southern British Columbia. J. Range Manage. 22:390-395.

Garman, E.H. 1973. Guide to the trees and shrubs of British Columbia. B.C. Prov. Museum Handb. No. 3.

Gilbert, N. 1980a. Comparative dynamics of a single-host aphid. I. The evidence. J. Anim. Ecol. 49:351-369.

_____. 1980b. Comparative dynamics of a single-host aphid. II. Theoretical consequences. J. Anim. Ecol. 49:371-380.

Gilbert, N. and A.P. Gutierrez. 1973. A plant-aphid-parasite relationship. J. Anim. Ecol. 42:323-340.

Glaze, N.C., M. Singh, and S.C. Phatak. 1987. Ornamental response to two methods of oxadiazon application. HortScience 22(2):265-268.

Gordon, J.C. and J.O. Dawson. 1979. Potential uses of nitrogen-fixing trees and shrubs in commercial forestry. Bot. Gaz. 140(Suppl.):S88-S90.

Granstrom, A. 1987. Seed viability of fourteen species during five years of storage in a forest soil. J. Ecol. 75:321-331.

Grant, W.F. and B.K. Thompson. 1975. Observations on Canadian birches, *Betula cordifolia*, *B. neoalaskana*; *B. populifolia*; *B. papyrifera*; and *B.* x *caerulea*. Can. J. Bot. 53:1478-1490.

Gratkowski, H. 1978. Herbicides for shrub and weed tree control in western Oregon. U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. PNW-77.

Gregory, R. A. 1966. The effect of leaf litter upon establishment of white spruce beneath paper birch. For. Chron. 42:251-255.

Grime, J. P. 1981. Plant strategies and vegetation processes. Wiley, Chichester.

Haeussler, S. and D. Coates. 1986. Autecological characteristics of selected species that compete with conifers in British Columbia: a literature review. Can. For. Serv. and B.C. Min. For. and Lands, FRDA Rep. 001.

Haeussler, S., J. Pojar, B.M. Geisler, D. Yole, and R.M. Annas. 1984. A guide to the Coastal Western Hemlock zone, Northern Drier Maritime subzone (CWHf), in the Prince George Forest Region, British Columbia. B.C. Min. For., Land Manage. Rep. No. 21. 165 p. (Abstract only).

_____. 1985. A guide to the Interior Cedar-Hemlock zone, Northwestern Transitional subzone (ICHg) in the Prince Rupert Forest Region, British Columbia. B.C. Min. For., Land Manage. Rep. No. 26. 262 p. (Abstract only).

Hall, J.W., D.G. Stout, and B. Brooke. 1987. Recovery of pinegrass after clipping (simulated grazing). Can. J. Plant Sci. 67:259-262.

Hamel, D.R. 1983. Forest management chemicals: a guide to use when considering pesticides for forest management. U.S. Dep. Agric. For. Serv., Agric. Handb. 585.

Hann, W.J. 1986. Evaluation of site preparation and conifer release treatments in North Idaho shrubfields. *In* Weed control in the interior west: Symp. Proc. D.M. Baumgartner, R.J. Boyd, D.W. Breuer, and D.L. Miller (editors). Feb. 5-7, 1985. Spokane, Wash. Coop. Ext. Serv., Wash. State Univ., pp. 115-119.

Harrington, C.A. and R.L. Deal. 1982. Sitka alder, a candidate for mixed stands. Can. J. For. Res. 12:108-111.

Heilman, P. 1983. Effects of surface treatment and interplanting of shrub alder on growth of Douglas-fir on coal spoils. J. Environ. Qual. 12:109-113.

Heilman, P. and G. Ekuan. 1982. Nodulation and nitrogen fixation by red alder and Sitka alder on coal mine spoils. Can. J. For. Res. 12:992-997.

Heninger, R.L. and D.P. White. 1974. Tree seedling growth at different soil temperatures. For. Sci. 20:363-367.

Hibbs, D.E. 1982. Gap dynamics in a hemlock-hardwood forest. Can. J. For. Res. 12:522-527.

Hickman, J.C. and M.P. Johnson. 1969. An analysis of geographical variation in western North American Menziesia (Ericaceae). Madrono 20(1):1-11.

Hitchcock, A.S. 1971. Manual of the grasses of the United States. 2nd ed. Vol. 1. Dover Publ. Inc., New York, N.Y.

Hitchcock, C.L., A. Cronquist, M. Ownbey, and J.W. Thomson. 1961. Vascular plants of the Pacific Northwest. Univ. Wash. Press, Seattle, Wash.

Horsley, S.B. and H.G. Abbott. 1970. Direct seeding of paper birch in strip clearcutting. J. For. 68:635-638.

Hosie, R.C. 1966. Native trees of Canada. Canada Dep. For. Rural Devel., Bull. 61, 6th ed., pp. 126, 132-135.

_____. 1973. Native trees of Canada. 7th ed. Fitzhenry and Whiteside Ltd. in cooperation with Can. For. Serv. and the Can. Gov. Publishing Cent., Don Mills, Ont.

_____. 1979. The alders. Sitka alder. Native trees of Canada. 8th ed. Fitzhenry and Whiteside Ltd. in cooperation with Can. For. Serv. and the Can. Gov. Publishing Cent., Don Mills, Ont., pp. 174-175.

Hulten, E. 1968. Flora of Alaska and neighbouring territories: a manual of the vascular plants. Stanford Univ. Press, Stanford, Cal.

Hungerford, R.D. 1984. Native shrubs: suitability for revegetating road cuts in northwestern Montana. U.S. Dep. Agric. For. Serv., Res. Pap. INT-331. 13 p.

Hyvarinen, M.J. 1968. Paper birch — its characteristics, properties, and uses: a review of recent literature. U.S. Dep. Agric. For. Serv., Res. Pap. NC-22.

Irwin, L.L. and J.M. Peek. 1979. Shrub production and biomass trends following five logging treatments within the Cedar-Hemlock zone of northern Idaho. For. Sci. 25:415-426.

Isaac, L.A. 1940. Vegetative succession following logging in the Douglas-fir region with special reference to fire. J. For. 38:716-721.

Iwaya-Inoue, M. and S. Kaku. 1983. Cold hardiness in various organs and tissues of Rhododendron species and the supercooling ability of flower buds as the most susceptible organ. Cryobiology 20:310-317.

James, G.I. and G.M. Courtin. 1985. Stand structure and growth form of the birch transition community in an industrially damaged ecosystem, Sudbury, Ontario. Can. J. For. Res. 15:809-817.

Jobidan, R. 1986. Allelopathic potential of coniferous species to old-field weeds in eastern Quebec. For. Sci. 32:112-118.

Johnson, E.A. 1975. Buried seed populations in the subarctic forest east of Great Slave Lake, Northwest Territories. Can. J. Bot. 53:2933-2941.

Johnston, A. and L.M. Bezeau. 1962. Chemical composition of range forage plants of the *Festuca scabrella* association. Can. J. Plant Sci. 42:105-115.

Jordon, J.S. and F.M. Rushmore. 1969. Animal damage to birch. *In* Birch Symp. Proc. U.S. Dep. Agric. For. Serv., NE For. Exp. Stn., pp. 155-163.

Kellman, M.C. 1969. Plant species interrelationships in a secondary succession in coastal British Columbia. Syesis 2:201-212.

_____. 1970. The viable seed content of some forest soil in coastal British Columbia. Can. J. Bot. 48:1383-1385.

Kelpsas, B.R. 1978. Comparative effects of chemical, fire, and mechanical site preparation in an Oregon coastal brushfield. M.Sc. thesis. Oreg. State Univ., Corvallis, Oreg. .

Kenady, R.M. 1978. Regeneration of red alder. *In* Utilization and management of alder. D.G. Briggs, D.S. DeBell, and W.A. Atkinson (compilers). U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. PNW-70, pp. 183-192.

Kimber, A.J., I.D. Pulford, and H.J. Duncan. 1978. Chemical variation and vegetation distribution on a coal waste tip. J. Appl. Ecol. 15:627-633.

Klinka, K., M.C. Feller, and R.K. Scagel. 1982. Characterization of the most productive ecosystems for the growth of Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) in southwestern British Columbia. B.C. Min. For., Land Manage. Rep. No. 9. 80 p.

Klinka, K. and A.M. Scagel. 1984. Selected ecological characteristics of some tree and shrub species in British Columbia: genera Juniperus, Taxus, Populus, Alnus, Betula, Quercus, Prunus, Rhamnus, Acer, Cornus, and Arbutus. Can. Cartographics Ltd., Coquitlam, B.C.

Krajina, V.J., K. Klinka, and J. Worrall. 1982. Distribution and autecological characteristics of trees and shrubs of British Columbia. Univ. B.C., Faculty of Forestry, Vancouver, B.C., pp. 95-96.

Kuhns, L.J. and C. Haramaki. 1980. An evaluation of 5 herbicides applied over liners representing 8 genera of ornamental plants. Proc. NE Weed Control Conf. 34:340-345.

Lafferty, R.R. 1972. Regeneration and plant succession as related to fire intensity on clear-cut logged areas in coastal cedar-hemlock type: an interim report. Can. For. Serv., Pac. For. Cent., Internal Report BC-33.

Laursen, S.B. 1984. Predicting shrub community composition and structure following management disturbance in forest ecosystems of the intermountain west. Ph.D. thesis, Univ. Idaho, Moscow, Idaho. 261 p.

Lloyd, D. 1984. Identification and interpretation of ecosystem units in the North Thomson-Shuswap Drainage Basins. First approx. B.C. Min. For., Res. Section, Kamloops Region. Kamloops, B.C. 103 p.

Logan, K.T. 1965. Growth of tree seedlings as affected by light intensity. I. White birch, yellow birch, sugar maple, and silver maple. Can. Dep. For. Publ. No. 1121.

Lowdermilk, W.C. 1925. Factors affecting reproduction of Engelmann spruce. J. Agric. Res. 30(11):995-1009.

Lust, N. and M. Mohammady. 1973. Regeneration of coppice. Sylva Gandavensis 39:1-28.

Lyons, C.P. 1952. Trees, shrubs and flowers to know in British Columbia. J.M. Dent and Sons Ltd., Vancouver, B.C.

McConnell, B.R. and J.G. Smith. 1970. Response of understory vegetation to ponderosa pine thinning in eastern Washington. J. Range Manage. 23:208-212.

McGee, C.E. and R.C. Smith. 1967. Undisturbed Rhododendron thickets are not spreading. J. For. 65(5):334-335.

McLean, A. 1967. Germination of forest range species from southern British Columbia. J. Range Manage. 20:321-322.

_____. 1969. Fire resistance of forest species as influenced by root systems. J. Range Manage. 22:120-122.

_____. 1970. Plant communities of the Similkameen Valley, British Columbia and their relationships to soils. Ecol. Mon. 40:403-423.

_____.(ed). 1979. Range management - handbook for British Columbia. Agric. Can. Res. Section, Kamloops, B.C., pp. 22, 60-61.

_____. 1983. Classification and management of the Douglas-fir pinegrass region. *In* Forestland grazing. Proc. Symp. B.F. Roche, Jr., and D.M. Baumgartner (editiors). Feb. 23-25, 1983, Spokane, Wash. Coop. Ext. Wash. State Univ, pp. 15-18.

McLean, A., S. Freyman, J.E. Miltimore, and D.M. Bowden. 1969. Evaluation of pinegrass as range forage. Can. J. Plant Sci. 49:351-359.

McLean, A., T.M. Lord, and A.J. Green. 1971. Utilization of the major plant communities in the Similkameen Valley, British Columbia. J. Range Manage. 24:346-351.

McLean, A. and E.W. Tisdale. 1960. Chemical compositions of native forage plants in British Columbia in relation to grazing practices. Can. J. Plant Sci. 40:402-423.

McNicol, R.J., B. Williamson, D.L. Jennings, and J.A.T. Woodford. 1983. Resistance to raspberry cane midge (*Resseliella theobaldi*) and its association with wound periderm in *Rubus crataegifolius* and its red raspberry derivatives. Ann. Appl. Biol. 103:489-495.

MacNaeidhe, F.S. and P.L. Curran. 1982. Weed colonisation of bogs taken into cultivation and seed dormancy of Polygonum invaders. Ir. J. Agric. Res. 21:199-209.

Marchant, C. and J. Sherlock. 1984. A guide to selection and propagation of some native woody species for land rehabilitation in British Columbia. B.C. Min. For. Res. Rep. RR84007-HQ.

Marks, P.L. 1975. On the relation between extension growth and successional status of deciduous trees of the northeastern United States. Bull. Torrey Bot. Club 102:172-177.

Marquis, D.A. 1966. Germination and growth of paper birch and yellow birch in simulated strip cuttings. U.S. Dep. Agric. For. Serv., Res. Pap. NE-54.

Marquis, D.A., J.C. Bjorkbom, and G. Yelenosky. 1964. Effect of seedbed condition and light exposure on paper birch regeneration. J. For. 62:876-881.

Mazurenko, M.T. 1979. Ecobiomorphs of Rhododendron aureum Georgi in the Magadan Province. Sov. J. Ecol. 10(2):114-120.

Miles, J. 1985. The ecological background to vegetation management. Brit. Crop Prot. Counc. Monogr. 30:3-20.

Miller, D.L. 1986a. Conifer release in the inland northwest - effects. *In* Weed control for forest productivity in the interior west: Symp. Proc. D.M. Baumgartner, R.J. Boyd, D.W. Breuer, and D.L. Miller. Feb. 5-7, 1985. Spokane, Wash. Coop. Ext. Serv. Wash. State Univ., pp. 17-24.

_____. 1986b. Conifer release in the inland northwest - chemical methods. *In* Weed control for forest productivity in the interior west: Symp. Proc. D.M. Baumgartner, R.J. Boyd, D.W. Breuer, and D.L. Miller. Feb. 5-7, 1985. Spokane, Wash. Coop. Ext. Serv., Wash. State Univ., pp. 109-113.

Miller, M. 1977. Response of blue huckleberry to prescribed fires in a western Montana larch-fir forest. U.S. Dep. Agric. For. Serv., Res. Pap. INT-188. Intermountain For. Range Exp. Stn. Ogden, Utah. 33 p.

Miller, M.M. and J.W. Miller. 1974. Succession after wildfire in the north Cascades national park complex. Ann. Tall Timbers Fire Ecol. Conf. 15:71-83.

Mitchell, W.R. and R.E. Green. 1981. Identification and interpretation of ecosystems of the Western Kamloops Forest Region. B.C. Min. For., Land Manage. Handb. No. 2.

Mitchell, W.W. 1968. On the ecology of Sitka alder in the subalpine zone of south-central Alaska. *In* Biology of alder. J.M. Trappe, J.F. Franklin, R.F. Tarrant, and G.M. Hansen (editors). U.S. Dep. Agric. For. Serv., Pac. NW For. Range Exp. Stn., Portland, Oreg., pp. 45-56.

Morgan, D.C. and H. Smith. 1979. A systematic relationship between phytochrome controlled development and species habitat, for plants grown in simulated natural radiation. Planta 145:253-258.

Morgan, P. 1984. Modeling shrub succession following clearcutting and burning. Ph.D. thesis. Univ. Idaho, Moscow, Idaho. 146 p.

Morris, W.G. 1970. Effects of slash burning in overmature stands of the Douglas-fir region. For. Sci. 16:258-270.

Mosquin, T. 1966. A new taxonomy for *Epilobium angustifolium* L. (Onagraceae). Brittonia 18:167-188.

Moss, E.H. 1936. The ecology of *Epilobium angustifolium* with particular reference to rings on periderm in the wood. Amer. J. Bot. 23:114-120.

Moss, E.H. 1959. Flora of Alberta. Univ. Toronto Press, Toronto, Ont.

Mueggler, W.F. 1965. Ecology of seral shrub communities in the cedar-hemlock zone of northern Idaho. Ecol. Monogr. 35(2):165-185.

Myerscough, P.J. 1980. Biological flora of the British Isles. No. 148. *Epilobium angustifolium* L. (*Chamaenerion angustifolium* (L.) Scop.). J. Ecol. 68:1047-1074.

Myerscough, P.J. and F.H. Whitehead. 1965. Comparative biology of *Tussilago farfara* L., *Chamaenerion angustifolium* (L.) Scop., *Epilobium montanum* L. and *Epilobium adenocaulon* Hausskn. I. General biology and germination. New Phyt. 65:192-210.

_____ . 1967. Comparative biology of *Tussilago farfara* L., *Chamaenerion angustifolium* (L.) Scop., *Epilobium montanum* L. and *Epilobium adenocaulon* Hausskn. II. Growth and ecology. New Phytol. 66:785-823.

Nazrul-Islam, A.K.M. 1983. Tissue water relations in a range of plant species and its ecological significance. Flora 174:329-337.

Neary, D.G., J.E. Douglass, and W. Fox. 1979. Low picloram concentrations in streamflow resulting from forest application of Tordon-10K. Proc. South. Weed Sci. Soc. 32:182-197.

Neary, D.G., J.E. Douglass, J.L. Ruehle, and W. Fox. 1984. Converting rhododendron-laurel thickets to white pine with picloram and mycorrhizae-inoculated seedlings. South. J. Appl. For. 8(3):163-168.

Nichols, G.E. 1934. The influence of exposure to winter temperatures upon seed germination in various native American plants. Ecology 15:364-373.

Nielsen, A.P. and R.C. Wakefield. 1978. Competitive effects of turfgrass on the growth of ornamental shrubs. Agron. J. 70(1-3):39-42.

Nilsen, E.T. 1985. Seasonal and diurnal leaf movements of *Rhododendron maximum* L. in contrasting irradiance environments. Oecologia 65:296-302.

_____. 1986a. Causes and significance of winter leaf movements in rhododendrons. Am. Rhododendron Soc. 40(1):14-15.

_____. 1986b. Quantitative phenology and leaf survivorship of *Rhododendron maximum* in contrasting irradiance environments of the Southern Appalachian Mountains. Am. J. Bot. 73(6):822-831.

Norby, R.J. and T.T. Kozlowski. 1983. Flooding and SO_2 stress interaction in *Betula papyrifera* and *B. nigra* seedlings. For. Sci. 29(4):739-750.

Oberbauer, S. and P.C. Miller. 1982. Effect of water potential on seed germination. Holarct Ecol. 5:218-220.

Ohmann, L.F., H.O. Batzer, R.R. Buech, D.C. Lothner, D.A. Perala, A.L. Schipper, Jr., and E.S. Verry. 1978. White (paper) birch: type description; and evaluation discussion. Some harvesting options and their consequences for the aspen, birch, and associated conifer forest types of the Lake states. U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. NC-48, pp. 12-14.

Olmsted, N.W. and J.D. Curtis. 1947. Seeds of the forest floor. Ecology 28:49-52.

Patterson, P.A., K.E. Neiman, and J.R. Tonn. 1985. Field guide to forest plants of northern Idaho. U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. INT-80. 246 p.

Peterson, E.B. 1965. The subalpine mountain hemlock zone. Part 1: Phytocoenoses. Ecol. West. North Am. 1:76-78.

Phillips, D.L. and W. Murdy. 1985. Effects of rhododendron (*Rhododendron maximum* L.) on regeneration of southern Appalachian hardwoods. For. Sci. 31(1):226-233.

Plocher, A.E. and K.L. Carvell. 1987. Population dynamics of rosebay Rhododendron thickets in the southern Appalachians. Bull. Torrey Bot. Club 114(2):121-126.

Pojar, J., R. Love, D. Meidinger, and R. Scagel. 1982. Some common plants of the sub-boreal spruce zone. B.C. Min. For., Land Manage. Handb. No. 6.

Pomerleau, R. and M. Lortie. 1962. Relationships of dieback to the rooting depth of white birch. For. Sci. 8:219-224.

Post, B.W., W.H. Carmean, and R.O. Curtis. 1969. Birch soil-site requirements. *In* Birch Symp. Proc. U.S. Dep. Agric. For. Serv., NE For. Exp. Stn., pp. 95-101.

Prasad, R. 1983. Some physiological and phytotoxic effects of herbicides on forest seeds and seedlings: I. Evaluation of herbicidal properties by a seed germination techniques. In Proc. Cone and Seed Insects Working Party Conf., H.O. Yales (editor). Athens, Ga.

Richardson, J. 1979. Relationships between natural reproduction of hardwoods and softwoods in western Newfoundland. Can. Fish. Environ., For. Serv. Nfld. For. Res. Cent., St. John's, Nfld., Info. Rep. N-X-166.

Ronco, F. 1970. Influence of high light intensity on survival of planted Engelmann spruce. For. Sci. 16(3):331-339.

Rowe, J.C. 1983. Concepts of fire effects on plant individuals and species. *In* The role of fire in northern circumpolar ecosystems. R.W. Wein and D.A. MacLean (editors). John Wiley & Sons, New York, N.Y., pp. 135-154.

Safford, L.O. 1982. Correlation of greenhouse bioassay with field response to fertilizer by paper birch. Plant Soil 64:167-176.

Safford, L.O. and M.M. Czapowskyj. 1986. Fertilizer stimulates growth and mortality in a young Populus-Betula stand: 10-year results. Can. J. For. Res. 16:807-813.

Sakai, A., L. Fuchigami, and C.J. Weiser. 1986. Cold hardiness in the genus Rhododendron. J. Am. Soc. Hortic. Sci. 111(2):273-280.

Salisbury, E. 1961. Weeds and aliens. Collins, London, England. 384 p.

Scherbatskoy, T., R.M. Klein, and G.J. Badger. 1987. Germination responses of forest tree seed to acidity and metal ions. Env. Exp. Bot. 27(2):157-164.

Schmidt, W.C. and J.E. Lotan. 1980. Phenology of common forest flora of the Northern Rockies — 1928 to 1937. U.S. Dep. Agric. For. Serv., Res. Pap. INT-259. 20 p.

Schmitt, M.D.C., M.M. Czapowskyj, L.O. Safford, and A.L. Leaf. 1981. Biomass and elemental uptake in fertilized and unfertilized *Betula papyrifera* Marsh. and *Populus grandidentata* Michx. Plant Soil 60:111-121.

Schopmeyer, C.S. 1974. Seeds of woody plants in the United States. U.S. Dep. Agric. For. Serv., Washington, D.C.

Scoggan, H.J. 1978. Flora of Canada. National Museum Nat. Sci. Publ. in Botany No. 7.

Shaw, M.W. 1984. *Rhododendron ponticum* — ecological reasons for the success of an alien species in Britain and features that may assist in the control. *In* Aspects of applied biology 5, 1984: weed control and vegetation management in forests and amenity areas. Wellesbourne, Warwick. Univ. of Nottingham, England, pp. 231-242.

Shigo, A.L. 1969. Diseases of birch. *In* Birch Symp. Proc.. U.S. Dep. Agric. For. Serv., NE For. Range Exp. Stn. pp. 147-150.

Shipton, W.A. and A.J.P. Burggraaf. 1982. Frankia growth and activity as influenced by water potential. Plant and Soil 69:293-297.

Solomon, D.S. and W.B. Leak. 1969. Stocking, growth and yield of birch stands. *In* Birch Symp. Proc.. U.S. Dep. Agric. For. Serv., NE For. Exp. Stn. pp. 106-118.

Stewart, R.E. 1974a. Budbreak sprays for site preparation and release from six coastal brush species. U.S. Dep. Agric. For. Serv., Res. Pap. PNW-176.

_____. 1974b. Repeated spraying to control four coastal brush species. U.S. Dep. Agric. For. Serv., Res. Note PNW-238.

_____. 1974c. Foliage sprays for site preparation and release from six coastal brush species. U.S. Dep. Agric. For. Serv., Res. Pap. PNW-172.

_____. 1975. Allelopathic potential of western bracken. J. Chem. Ecol. 1:161-169.

_____. 1978. Origin and development of vegetation after spraying and burning in a coastal Oregon clearcut. U.S. Dep. Agric. For. Serv., Res. Note PNW-317.

Stewart, R.E. and T. Beebe. 1974. Survival of ponderosa pine seedlings following control of competing grasses. Proc. Wes. Soc. Weed Sci. 27:55-58.

Stickney, P.F. 1980. Data base for post-fire succession, first 6 to 9 years, in Montana larch-fir forests. U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. INT-62. Intermountain For. Range Exp. Stn. Ogden, Utah. 131 p.

_____. 1981. Vegetative recovery and development. *In* Clearcutting and fire on the larch/Douglas-fir forests of western Montana - a multifaceted research summary. N.Y. DeByle (editor) U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. INT-99. pp. 33-40.

_____. 1985. Database for early postfire succession on the Sundance Burn, northern Idaho. U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. INT-189.

_____. 1986. First decade plant succession following the Sundance forest fire, northern Idaho. U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. INT-197.

Stout, D.G. and B. Brooke. 1987. Tiller production of grazed and clipped pinegrass. Can. J. Plant Sci. 67:503-508.

Stout, D.G, J. Hall, B. Brooke, and A. McLean. 1981. Influence of successive years of simulated grazing (clipping) on pinegrass growth. Can. J. Plant Sci. 61:939-943.

Sutton, R.F. 1978. Glyphosate herbicide: an assessment of forestry potential. For. Chron. 54:24-28.

Svejcar, T. 1986. Comparative water relations of *Carex geyeri* and *Calamagrostis rubescens*. Bot. Gaz. 147:71-77.

Sylvester, T.W. and R.W. Wein. 1981. Fuel characteristics of arctic plant species and simulated plant community flammability by Rothermel's model. Can. J. Bot. 59:898-907.

Szczawinski, A.F. 1962. The heather family (Ericaceae) of British Columbia. B.C. Prov. Museum Handb. No. 19, Victoria, B.C.

Tabbush, P.M. and J.S.P. Sale. 1984. Experiments on the chemical control of *Rhododendron ponticum* L. *In* Aspects of applied biology 5, 1984: weed control and vegetation management in forests and amenity areas. Wellesbourne, Warwick, Univ. Nottingham, England, pp. 243-253.

Tang, Z.C. and T.T. Kozlowski. 1982. Some physiological and growth responses of *Betula papyrifera* seedlings to flooding. Physiol. Plant. 55:415-420.

Tarrant, R.F. 1983. Nitrogen fixation in North American forestry: research and application. *In* Biological nitrogen fixation in forest ecosystems: foundations and applications. J.C. Gordon and C.T. Wheeler (editors). Martinus Nijhoff/ Dr. W. Junk, pp. 261-277.

Taylor, R.L. and B. MacBryde. 1977. Vascular plants of British Columbia: a descriptive resource inventory. Univ. B.C., Bot. Garden Tech. Bull. No. 4.

Taylor, T.M.C. 1973. The rose family of British Columbia. B.C. Prov. Museum Handb. No. 30, Victoria, B.C.

Tiedemann, A.R. and G.O. Klock. 1974. Development of vegetation after fire, seeding, and fertilization on the Entiat experimental forest. Tall Timbers Fire Ecol. Conf. 15:171-192.

Turner, D.J. and W.G. Richardson. 1979. Herbicide evaluation for forestry uses. Report on Forest Research 1979. London, U.K. HMSO 55-57.

Ugolini, F.C. 1968. Soil development and alder invasion in a recently deglaciated area of Glacier Bay, Alaska. *In* Biology of alder. J.M. Trappe, J.F. Franklin, R.F. Tarrant, and G.M. Hansen (editors). U.S. Dep. Agric. For. Serv., PNW For. Range Exp. Stn. pp. 115-140.

U.S. Department of Agriculture. 1974. Seeds of woody plants of the United States. U.S. Dep. Agric. For. Serv., Agric. Handb. No. 450.

van Andel, J. 1975. A study on the population dynamics of the perennial plant species *Chamaenerion angustifolium* (L.) Scop. Oecol. 19:329-337.

van Andel, J. and H.J.M. Nelissen. 1973. Applicability of factor analysis in autecological research, with particular reference to *Chamaenerion angustifolium* (L.) Scop. Acta Bot. Neerl. 22:599-607.

_____ . 1979. Nutritional status of soil and plant species in several clearings in coniferous woods compared to that in two related habitats. Vegetatio 39:115-121.

van Andel, J. and J. Rozema. 1974. An experiment in reproduction from seed within existing populations of *Chamaenerion angustifolium* (L.) Scop. Plant Soil 41:415-419.

van Cleve, K., O.W. Heal, and D. Roberts. 1986. Bioassay of forest floor nitrogen supply for plant growth. Can. J. For. Res. 16:1320-1326.

Viereck, L.A. and E.L. Little. 1972. Alaska trees and shrubs. U.S. Dep. Agric. For. Serv., Agric. Handb. No. 410, pp. 134-140.

_____ . 1986. Alaska trees and shrubs. U.S. Dep. Agric. For. Serv. Agric. Handb. No. 410.

Voth, E.H., C. Meser, and M.L. Johnson. 1983. Food habits of *Arborimus albipes*, the white-footed vole, in Oregon. Northwest Sci. 57:1-7.

Wali, M.K. 1969. Vegetation-environment relationships of sub-boreal spruce zone ecosystems in British Columbia. Ph.D. thesis. Univ. B. C., Vancouver, B.C.

Wangberg, J.K. 1975. Biology of the thimbleberry gallmaker *Diastrophus kincaidii*. Pan-Pacific Entomologist 51:39-48.

Warren, L.F. 1982. Garlon herbicides control hardwoods, release conifers in western forests. Industrial Vegetation Manage. 14:18-21.

Watson, L.E., R.W. Parker, and D.F. Polster. 1980. Manual of plant species suitability for reclamation in Alberta. Vol. II - Forbs, shrubs and trees. Land Conserv. and Reclamation Council, Gov. Alta. Report #RRTAC 80-5.

Wein, R.W. and L.C. Bliss. 1973. Changes in arctic Eriophorum tussock communities following fire. Ecol. 54:845-852.

Weinberger, P., L. Pomber, and R. Prasad. 1978. Some toxic effects of fenitrothion on seed germination and early seedling growth of jack pine, spruce, and birches. Can. J. For. Res. 8:243-246.

Wile, B.C. 1981. A test of five herbicides and three methods of ground application for cleaning young stands and clearcut areas. Can. For. Serv., Dep. Environ., Maritimes For. Res. Cent., Fredericton, N.B. Info. Rep. M-X-126.

William, R.D., L.C. Burrill, R. Parker, D.G. Swan, S.W. Howard, and D. Kidder. 1987. Pacific Northwest weed control handbook. Exten. Serv. Oreg. State Univ., Wash. State Univ., and Univ. Idaho. 239 p.

Wittinger, W.T., W.L. Pengelly, L.L. Irwin, and J.M. Peek. 1977. A 20-year record of shrub succession in logged areas in the Cedar-Hemlock zone of northern Idaho. Northwest Sci. 51:161-171.

Wright, H.A. 1972. Shrub response to fire. *In* Wildland shrubs — their biology and utilization. C.M. McKell, J.P. Blaisdell, and J.R. Goodin (editors). U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. INT-1, pp. 204-217.

Yarie, J. 1978. The role of understory vegetation in the nutrient cycle of forested ecosystems in the Mountain Hemlock biogeoclimatic zone. Ph.D. thesis. Univ. B.C., Faculty of Forestry, Vancouver, B.C. 176 p.

Zasada, J.C. 1971. Natural regeneration of interior Alaska forests - seed, seedbed, and vegetative reproduction considerations. *In* Proc. Symp. on Fire in the Northern Environment. C.W. Slaugher, R.J. Barney, and G.M. Hansen (editors). U.S. Dep. Agric. For. Serv.

Zasada, J.C., R.A. Norum, R.M. Van Veldhuizen, and C.E. Teutsch. 1983. Artificial regeneration of trees and tall shrubs in experimentally burned upland black spruce/feather moss stands in Alaska. Can. J. For. Res. 13:903-913.